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THE UNIVERSITY OF ALBERTA

To

my Grandfather and Father

who taught me to appreciate

the diversity of life.



PETER G. NEVILL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES OF

PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGY

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1970





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HIGH ARCTIC INSECT-FLOWER RELATIONS:

THE INTER-RELATIONSHIPS OF ARTHROPODS AND FLOWERS

AT LAKE HAZEN, ELLESMERE ISLAND, N.W.T., CANADA

by



PETER G. KEVAN

A THESIS

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ABSTRACT

The environment of the Hazen Camp study area is described and in relation to it the adaptations of insects and plants are considered. In the arctic the inter-relationships between arthropods and flowers have hitherto been little studied. In 1967, over 2,500 observations of individual arthropods, involving about 44% of the about 250 species known from Hazen Camp, on blooms were made. The activity, amount of pollen dusting, ingested pollen and nectar were observed for each specimen, and the females were examined for the stage of development of their ovarian follicles. At least 36% of the Hazen insect fauna imbibes nectar. Each species of arthropod is treated separately as no general patterns of their biologies and of the importance of flowers as food sources in reproduction are evident. More work would probably show all species of Lepidoptera, Diptera-Brachycera, Hymenoptera, and some families of Diptera depend on nectar for food. Pollen feeding is restricted to 9 species of insect, from Collembola to bumblebees. Pollen is vital to these species as food for ovarian maturation and body maintenance. The larvae of some insects are dependent on ovarian tissue for food. At least 3 predatory species of arthropods use flowers as ambush sites. Some insects (Chironomidae) may use groups of plants in flowers as swarm markers, and others may copulate within inflorescences.

Blooms of the about 75 dicotyledons at Hazen Camp show the same entomophilous characteristics as blooms elsewhere. Yellow (insect-red) inflorescences with or without ultraviolet (insect-blue) parts, and with circumferences greater than 3.0 cm are most visited. Purple and white inflorescences are well visited only when yellow ones are not in bloom. Floral movement and figure numeral play small roles. Groups of small





flowers anthia, are regarded as large and are visited according to their colour. Visual honey guides are unimportant, although structural guides (e.g. of *Pedicularis* spp.) are used by insects. Some insects use scent at close range. The characteristic odours of some inflorescences and plants may be unattractive. Scent may be the most important attractant in pistillate catkins of *Salix arctica*. There is strong correlation between the amount and accessibility of nectar and entomophily of blooms.

Elevated temperatures in the 5 types of blooms vary from about 2 C to over 10 C under optimal conditions. Parabolic reflectors, the hottest type focus heat at the stigmas. Insects bask there and may attain body temperature excesses between 5 and 17 C. Heliotropism of some blooms extends the period of maximum possible temperature excess.

Some plants are entirely dependent on insects for pollination and seed set, others are partially dependent for maximum seed set, while others set seed independently of insect pollen vectors. Some *Pedicularis* spp. are entirely dependent on bumblebees; pleomorphic flowers rely on Diptera, and to a lesser extent bumblebees and Lepidoptera. Diploidy is more common in outcrossing species of dicotyledons. There are regional differences in the success of seed set in *D. integrifolia* which I conclude reflect the availability of pollinators.

The dependence of many arctic insects on flowers for nutrition and the now proved dependence of some common arctic plants on insects for propagation are of great significance in biogeography.





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## AUTOBIOGRAPHICAL SKETCH

I was born on 17 June 1944 in Edinburgh, Scotland. For a few years I lived in Kenya, where my father worked on locust control research. I started my education in England, and attended 3 schools, the last being The Becket School, Westbridgford, Nottingham. When I was 14, the family came to Canada, and I completed my schooling at Macdonald High School, Quebec in 1961.

I was admitted to McGill University, where I undertook a joint honours course in Zoology and Mathematics. In my third year I dropped mathematics and continued in zoology, being awarded my B.Sc. with Honours in Zoology in 1965.

During the summers of my undergraduate years I worked for the Canada Department of Agriculture in Entomology Research Institutes. The first 2 summers were spent at Belleville, Ontario, where I worked on problems in biological control of mosquitoes and aphids. During the third summer I worked at the Entomology Research Institute, Ottawa, Ontario on the genetics of a small parasitic wasp. This experience provided the topic for my undergraduate thesis: "Spermatogenesis of an Arrhenotokous Insect, *Dahlbominus fuscipennis* (Zetterstedt, 1838) (Hymenoptera: Eulophidae).

By this time I was well soaked in Entomology and Zoology, and was following in the footsteps of my Grandfather and Father. I was also much inclined to outdoor life, and spent almost all my extra-curricular time with the McGill Outing Club. I became president of this club in my final undergraduate year. While with the Outing Club I met several people who had worked in Canada's arctic. My imagination





was bent in that direction. I wanted to combine my wish to work in the arctic with my interest in broadening my biological and entomological interests. Thus I sought admission as a graduate student under Dr. B. Hocking at the University of Alberta to study insect-flower relations in the high arctic.



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Aim

*The aim of this study is to determine the importance of insect-flower relations to both plants and insects, but more especially to the latter, in a high arctic community.*

*All facets of the arctic environment must be touched upon to understand how life carries on under such rigorous conditions, and how life can take advantage of temporally and spatially localized ameliorations in this environment.*

*Such ameliorations are physical, as in the microclimate, and biological, as in places to feed, shelter, mate, and oviposit; necessarily the two overlap. All these factors, essential to insect life in the high arctic, may be encountered within the corollas of flowers. Thus all aspects of flower biology of possible importance to insects are considered.*



PART I  
PHYSICAL ENVIRONMENT

I.1. Localities

Most of this work was done at Hazen Camp ( $81^{\circ} 49' \text{ N.}$ ,  $71^{\circ} 18' \text{ W.}$ ) on northern Ellesmere Island (Fig. 1 and 2). The camp is situated on a small sandy point about half way along the north shore of Lake Hazen. The study area (Fig. 3) was delimited, and the different habitats in the area of about  $23.5 \text{ km}^2$  described by Savile (1964). Within this area most of my work was done in the rectangle southeast of Mount McGill between Blister Creek and the Snow Goose River delta, about  $11 \text{ km}^2$ .

Many single day excursions were taken away from the study area, particularly behind, and on, the nearer peaks of the Garfield Range (Mount Omingmak to the east, Mount McGill, and an unnamed peak to the west). Some studies were undertaken at Gilman Camp ( $81^{\circ} 54' \text{ N.}$ ,  $69^{\circ} 30' \text{ W.}$ ) during 1966 and 1967. Here, although the plants are the same species as in the Hazen Camp area, some of the communities are quite different. Tanquary Fiord ( $81^{\circ} 24' \text{ N.}$ ,  $76^{\circ} 55' \text{ W.}$ ) was also used as a base for a short time in 1966 and 1968. The plant communities in this area are quite similar to those at Hazen Camp, except for some strand vegetation; the plant habitats have been reported on by Brassard (1968). In 1968 a hike between Hazen Camp and Tanquary Fiord, and return (some 250 km) gave me valuable insight into migration and dispersal in the area.







Figure 1. Canada (Relief).

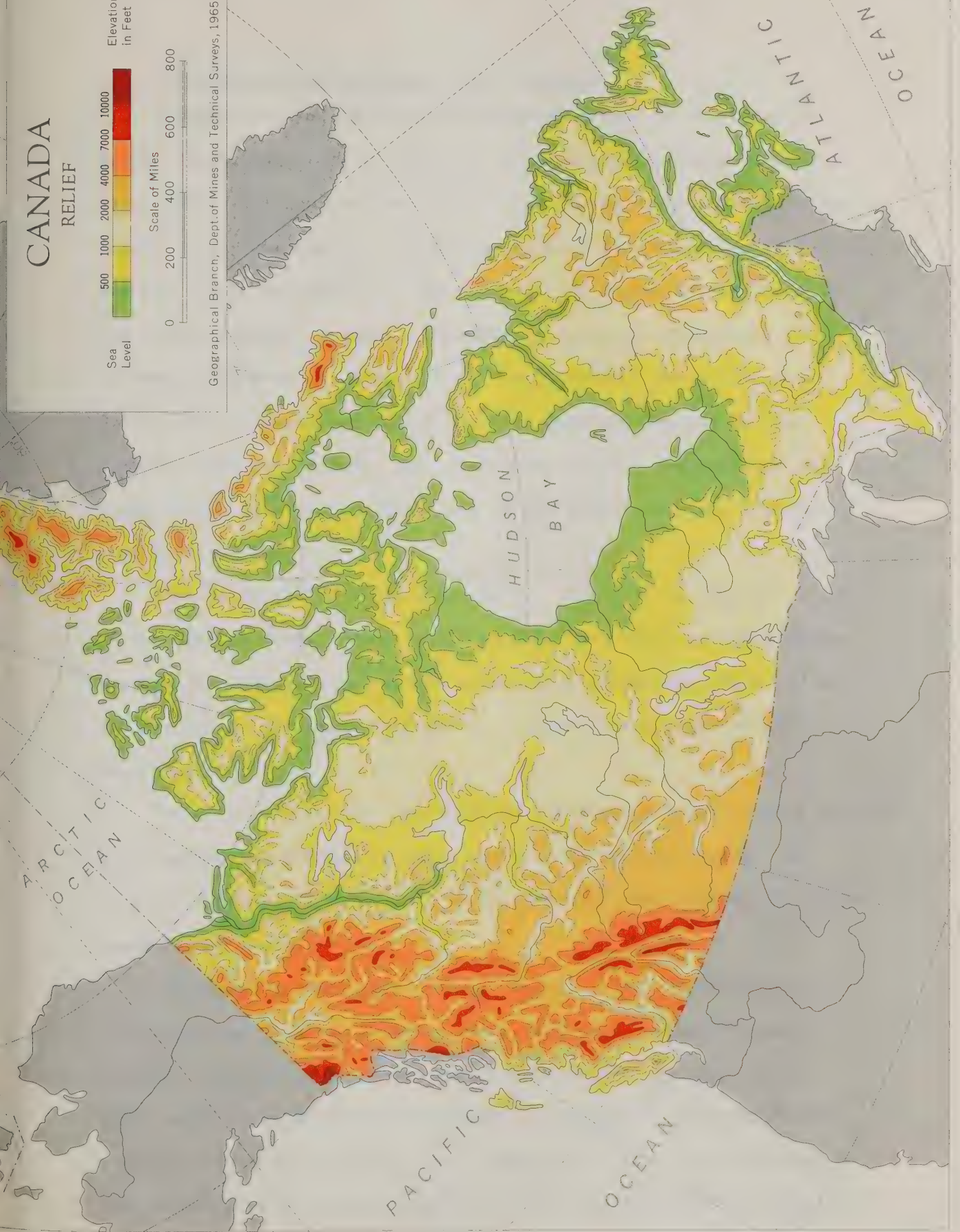
# CANADA

## RELIEF

Sea Level  
500 1000 2000 4000 7000 10000  
Elevation in Feet

Scale of Miles  
0 200 400 600 800

Geographical Branch, Dept. of Mines and Technical Surveys, 1965.





## I.2. Geography, Geomorphology, and Glaciation

Ellesmere Island is the most northerly island in the Canadian Arctic Archipelago, and is included in the Queen Elizabeth Islands. Its northern ice cap overlies the British Empire Range and the United States Range, the peaks of which rise to over 2600 m and appear through the ice cap as nunataks. To the south of the United States Range is the Garfield Range, a chain of smaller (about 1300 m) isolated peaks between which several large rivers, the Turnstone, Henrietta, Snow Goose, Abbé, Gilman, and Turnabout, flow from the ice cap and its glaciers into Lake Hazen. Two other major rivers, the Very and the Adams, drain into the southwest end of the lake. Many small streams also feed the lake.

Lake Hazen is 158 m above sea level. It is 78 km long and 11 km at its maximum width, oriented ENE to WSW. The southern shore slopes up onto the Greely-Hazen Plateau which rises to between 500 m and 800 m. Further to the south rise the ice capped Victoria and Albert Mountains.

The only outlet from Lake Hazen is the Ruggles River flowing through the Greely-Hazen Plateau 29 km to the head of Chandler Fiord. In previous times Black Rock Vale, 35 km east, may have drained the Lake Hazen trough (Smith, 1961).

Lake Hazen is very deep (263 m; Deane, 1959). Because of this, its large size (greater than any other lake in the Queen Elizabeth Islands), and the shape of its floor, Smith (1961) states that it seems unlikely to have been caused by glacial scour, and tentatively suggests that a second fault line, parallel to that at the southern edge of the Garfield Range, may be the cause. Deane (1959) preferred







Figure 2. Northern Ellesmere Island (from Brassard, 1968).

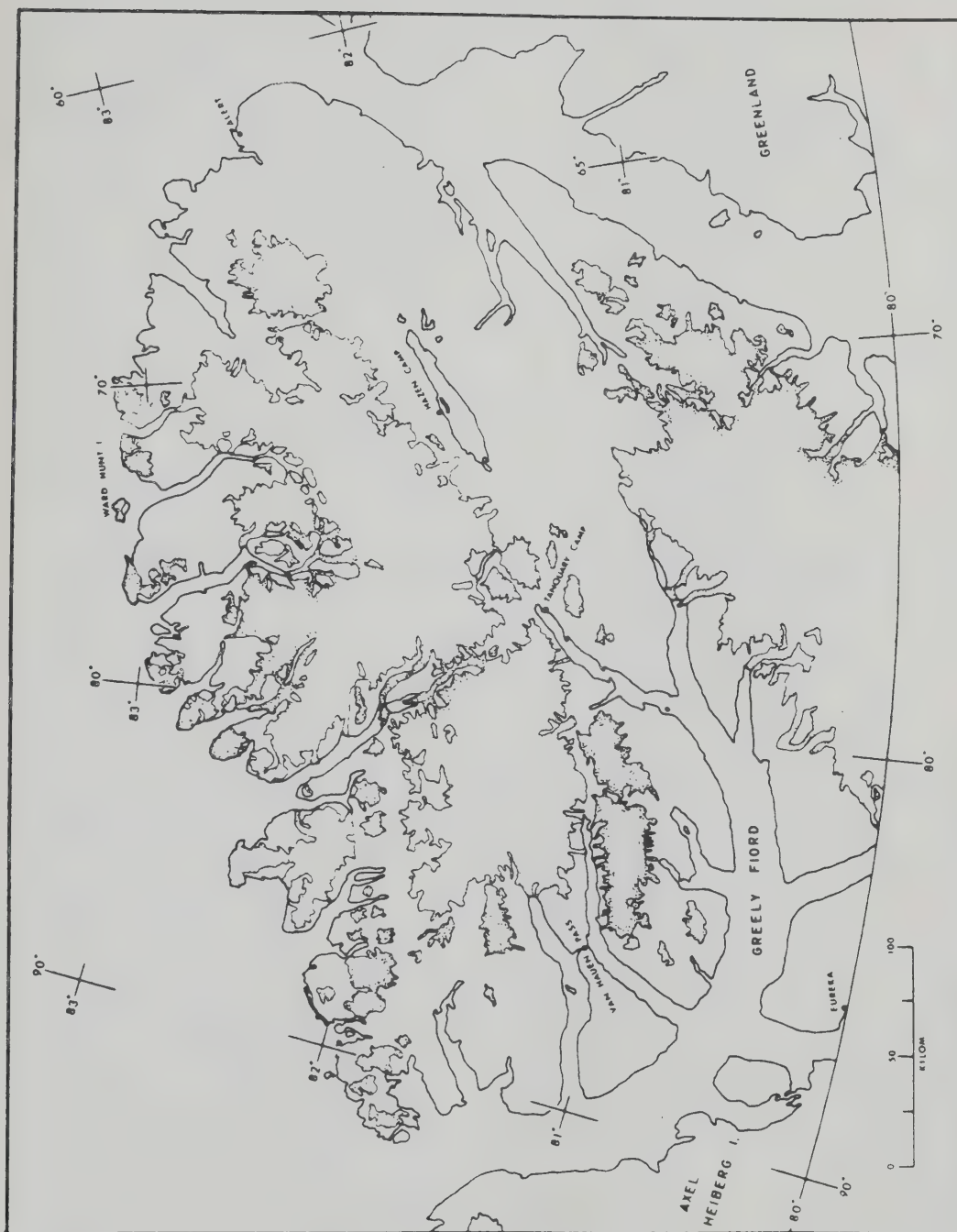
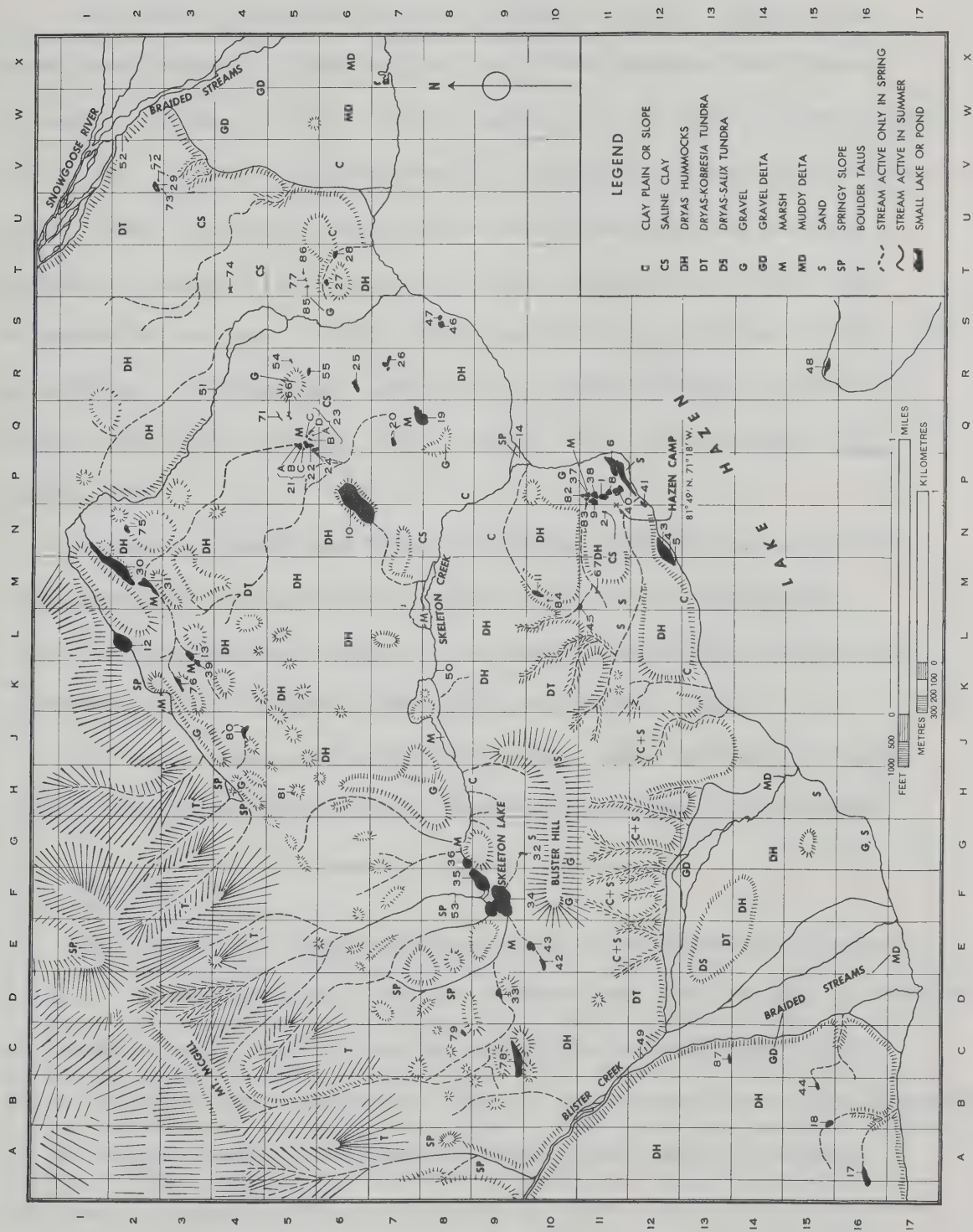








Figure 3. Hazen Camp study area (from Savile, 1964).





the glacial scour theory for its origin. Both authors may be correct.

Koch (1928) considers that the northern half of Pearyland has never been covered by ice, and Gelting (1934) upholds this view on botanical evidence. Taylor (1956) states that the whole of the Canadian arctic was overrun by Pleistocene ice which also covered all of Greenland. Smith (1961) concludes from erratics and striae that the whole of northern Ellesmere Island must have been glaciated on at least one occasion in the past. Savile (1964) specifically mentions the Wisconsin glaciation. Evidence for refugia in the Queen Elizabeth Islands is inconclusive (*cf.* Beschel, 1961; Savile, 1961; MacPherson, 1965; Leech, 1966).

Terracing around Lake Hazen led Savile (1964) to state that the lake level was 60 m above its present level during deglaciation. These terraces are too complex to be readily explained by lacustrine processes, and are probably kame terraces (Smith, 1961).

All in all, the glacial history of the Queen Elizabeth Islands is far from clear, and does not elucidate biogeographical problems.

### I.3. Geology

Christie (1964) described the geology of northeastern Ellesmere Island. In the immediate vicinity of Hazen Camp the low land is underlain by sandstone and shale of Mesozoic and Permo-Carboniferous origin. These deposits form Blister Hill (400 m) and the small but steep foothills of the nearer peaks of the Garfield Range (Mount McGill and Mount Omingmak). These foothills run along the first fault line. The rocks here erode rapidly and give rise to sand and clay, characteristic of the soils in the area. The mountains of the Garfield Range are composed of fairly resistant Silurian rocks of the Cape Rawson group.



These rocks shatter with frost action into boulders and slabs rather than into fine particles. Thus, the summer run-off from south facing talus slopes is below the surface, which is left arid and almost devoid of plant life. These talus slopes store early spring run-off frozen below the surface, and liberate it as warming penetrates through the summer.

#### I.4. Soils

Yong (1961) and Yong *et al.* (1960) studied the mechanical properties of the soils. They found that the active layer was about 60 cm in late August, while Leech (1966) reported, for the same month, but in 1963, that soil was unfrozen to a depth of 74 cm. Such a discrepancy would be expected unless the location were carefully standardized.

Day (1964), working in relation to Savile's (1964) previous study of the plant communities and habitats, classifies the soils as "regosols" as there is no significant development of genetic horizons. The organic content of the soils is low, varying between 0.3% and 19.6%; and the pH tends to be basic, lying between 7.3 and 8.7 (only 2 readings of acidic soils are given).

The ground is covered with frost cracks and heaves of widely varying dimensions. Above the ice wedges of the polygons the ground remains damp, and supports more plant life than the ground in the immediate vicinity. Yong *et al.* (1962) suspect that hummocks are produced from small polygons about 25 cm across, which under the cyclic action of freezing, thawing, wetting, drying, shrinking, and cracking become more pronounced (see also Troll, 1958). Hummocks become higher when covered by vegetation (particularly *Dryas integrifolia*) as a





result of its binding and protecting the soil against further erosion and drying. Hummocks occur more often in clay and silt soils, and become especially high in wet areas where snow drifts lie late in the spring. This occurs at the base of slopes where presumably as a result of the greater water availability, there is considerable growth of *Dryas integrifolia*. Such areas tend to be protected from wind and are much frequented by insects, many visiting the flowers of *Dryas integrifolia*.

Factors such as mineral and nitrogen contents of the soils have not been studied. Generally nitrification is low, but in areas of great animal activity, around fox dens, birds roosts, and human habitation, the flora is more diverse and luxuriant.

Although the bed rock is of paramount importance in considering the soils of this area it is obvious that the climate greatly influences soil formation, not only in the differences in its action from place to place, but also in its impression on the plants with their modifying effect on soil structure, composition, and formation. Animals play a small and local rôle.

### I.5. Meteorology

The climate of arctic tundra has been recently reviewed by McKay *et al.* (1970). The weather at Hazen Camp, Tanquary Fiord, and Eureka is much more benign than at most places in the arctic islands. Alert to the northeast has far more severe weather (Jackson, 1959).

#### I.5.1. Wind

The prevailing wind over Lake Hazen is northeasterly (Greely, 1888; Jackson, 1959). The wind speed is low, less than 2.25 mps for 75% of the time at 13 m (Jackson, 1959). This is due to the sheltering



effect of the mountains to the northwest and the thermal stability of the air in the Lake Hazen trough (Jackson, 1965). On the rare occasions when wind speeds exceed about 7 mps the fine glacial loess in the deltas of the Very, Adams, Macdonald, and Abbe rivers (all of which are visible from the top of Blister Hill) lifts, resulting in low but extensive dust storms.

Vertical gradients of wind speed are discussed by Geiger (1965). Jackson (1959) shows that at Hazen Camp the wind speed at 300 m is reduced 30% compared with the speed at 13 m. Within the first 30 cm wind reduction must be more evident as surface drag increases (cf. Geiger, 1965). Low wind speeds lessen turbulent mixing of the air. This allows the air in the first  $\frac{1}{2}$  meter or so above the ground to become more warmed than in windier localities. These considerations are important to the biology of the area, as within the zone very close to the soil surface (0-15 cm, Savile (1964)) most plant and insect activity occurs.

#### I.5.2. Radiation Climate, General

The solar constant is defined by Gates (1962) as "the amount of energy per unit time from the sun incident upon a surface placed outside the earth's atmosphere perpendicular to the sun's rays at the mean distance of the earth from the sun." Its value is about 2.00 cal/cm<sup>2</sup>/min (cf. Johnson, 1954).

The amount of solar radiation reaching the surface of the earth depends on the angle of solar elevation, and atmospheric transparency. Local variations of radiation climate depend on the slope and aspect of the ground. The radiation climate of the arctic has recently been reviewed by Gavrilova (1963) on the basis of actinometric measurements, mainly by the U.S.S.R. Ahrensbrak (1968) has studied the summer radiation



climate on the Canadian tundra.

Because of the continuous daylight, and the high atmospheric transmission (0.8; Gavrilova, 1963) due to little dust and moisture, the mean amounts of direct solar radiation per day in the arctic are only slightly less (and may be more) than in temperate and tropical regions. Figure 4, curves 1, 2, and 6 show the relation between solar elevation, undepleted radiation, and the time of year.

#### 1.5.2.1. Solar radiation and cloud cover

Stratocumulus clouds are the dominant type during the summer over northern Ellesmere Island. They do not deplete solar radiation as much as would be expected because, in the arctic, these clouds are often thin and low in moisture; hence they have high transmissions and diffusing capacities. In fact the diffuse radiation from them may exceed  $1 \text{ cal/cm}^2/\text{min}$ , but is more usually between 0.3 and  $0.5 \text{ cal/cm}^2/\text{min}$  (Gavrilova, 1963). Vowinkel (1964) has shown a greenhouse effect by arctic cloud cover.

#### 1.5.2.2. Cloudiness and hours of sunshine

The northeastern part of the arctic archipelago is the least cloudy region of the arctic. This is because of the prolonged influences of anticyclones which make the mean annual cloudiness in the region between Axel Heiberg Island and Pearyland 45-48% (Gavrilova, 1963). Barry (1964) states that at Tanquary Fiord anticyclonic spells in July gave only  $1/8$  or less cloud cover. The winter is the least cloudy time of the year, but as cyclonic activity is renewed in the spring so cloudiness increases to a maximum in late summer (Rae, 1951; Barry, 1964).





Observations at Lake Hazen in May and early June show "almost perpetual sunshine" (Deane, 1958). This is confirmed by Lotz (1958) who showed that the area received 80.3% of the possible sunshine in May, and 88.9% from June 1 to June 19. Lotz (1958) and Jackson (1959) divide the summer into two phases; the early phase from late May to mid-June with high sunshine totals, and the late phase from mid-June on with lower totals (June 20-30 with 60% of total possible). From the data presented by Lotz (1958, 1959), Jackson (1959, 1963), and Sagar (1960) it can be seen that Lake Hazen receives about 50% of the total possible sunshine during the biologically active season (of Corbet, 1966a); this probably is a very high figure for the arctic (Savile, 1964).

#### I.5.2.3. Summary

The Lake Hazen area has a continental climate. There is more sunshine, and lighter cloud cover depletes radiation less than in more southerly and coastal areas. This greater summer radiation, combined with the thermal stability and sheltered locale, result in comparatively warmer weather. This may, in part, be responsible for the richness of the flora and fauna.

#### I.5.3. Albedo of the Arctic Landscape

Air temperatures in the summer are controlled by insolation warming (Longley, 1958; Jackson, 1959). The air itself absorbs very little radiation. It becomes warmed by heat conducted from the surface of the earth, and subsequent convective mixing.

The amount of radiation which the earth's surface absorbs is inversely proportional to its albedo, that is, the percentage of



incident radiation reflected. The albedo of fresh snow is about 85% (List, 1968), and although this greatly increases the amount of diffuse radiation through reflection, it detracts greatly from the heating of the terrestrial environment (Geiger, 1965). As snow ages its albedo decreases with increases in the amount of dirt in it and compactness of its crystal structure. The albedo may drop to as low as 40% (Geiger, 1965; List, 1968). With the increase in absorbed radiation the snow soon melts, and patches of exposed ground warm rapidly, hastening the thaw. The snow gone, the albedo of the earth's surface drops to between 15 and 18% over the remains of the previous summer's vegetation, and is between 12 and 21% as the plants turn green as summer advances (Nekrasov, 1958; McKay *et al.*, 1970).

Although the incoming radiation at the earth's surface decreases due to the increase in cloud and the passing of the sun through its zenith, absorbed radiation shows a rapid increase and the radiation balance becomes positive (Fig. 4). Then air temperature (in a Stevenson screen) starts to rise sharply (Fig. 4, curves 3 and 8).

#### I.5.4. Annual March of Temperature, Solar Elevation, and Radiation Climate

The sun remains completely below the theoretical horizon from 16 October until 26 February (Anon, 1945) so that insolation is essentially nil, and the radiation balance is negative throughout this period (Fig. 4 curves). In the time of the autumn twilight (4 September to 16 October) the mean air temperature falls steadily to freezing, and continues to drop until the end of October when air temperatures are in the minus thirties C (-35 C for ten day mean (Jackson, 1961b)). The winter minimum at Hazen Camp may fall as low as -60 C. Such



extreme cold cannot have any additional effect on the survival of terrestrial plants and invertebrates, as they must be frozen throughout the winter.

Spring twilight lasts from 26 February to 10 April. There is a lag in the warming of the environment as heating is not enough to compensate for the outgoing radiation (Longley, 1958). Rapid warming does not start until about 1 April, coincidental with the onset of continuous daylight. Then the radiation balance becomes positive. The warming trend continues markedly until about 10 June, coincidental with the resumption of cyclonic weather. Both Longley (1958) and Jackson (1959) conclude that rapid spring warming is due to insolation control of air temperature, as shown in Fig. 4. Synoptic events are of minimal importance at this time (Jackson, 1959).

By the time the "active season" (of Corbet, 1966a) starts in early June, the steep rise in air temperature has ended, and the air temperatures in a Stevenson screen remain above freezing. Air temperatures then increase gradually, but not steadily, to reach a maximum in early August (the warmest day may be any time between 30 June and 3 August). The July mean is usually above 4.5 C, the average for 1962-1966 being 6 C (Corbet, 1967a).

During the "active season" synoptic events have a great influence on the radiation balance. Cloudiness, particularly, makes for a flattening of the spring-summer temperature curve as compared with the curves describing solar altitude, undepleted radiation, absorbed radiation, and radiation balance (Fig. 4).

#### I.5.5. The "Active Season"

The term "active season" was used by Corbet (1966a) and is based





on observations on insect activity. The period starts in early June and lasts through late August (Corbet, 1966a).

The active season lasts over the period when the temperature of the air (as recorded in a Stevenson screen) remains above 3.5 C. This places the "active season" exactly between the "frost-free season" and the "growing season" (as used by Corbet, 1967a). The last term is defined by Boughner (1964) to be the period during which the daily mean equals or exceeds 5.4 C. It probably has little relevance in the arctic where biological activity is known to commence at lower temperatures than at lower latitudes.

The "active season" starts with the advent of clouds and cyclonic activity, and lasts throughout the period when synoptic events greatly influence the weather. This short 7 week period is then, the time of maximum temperatures and positive radiation balance.

#### I.5.6. Micrometeorology, General

The earth's surface is heated by solar radiation according to the albedo, specific heat, and thermal conductivity of the surface. Some values for the above properties of natural substances, such as rocks and soils, are given by List (1968). The heat so gained by the ground will be liberated as long wave radiation according to the Stefan-Boltzman law, or it will be used up for evaporation, or be conducted into the air molecules of the boundary layer and thence distributed into the atmosphere by convective mixing.

The lapse rate of the air close to the ground is often greater than the dry adiabatic lapse rate ( $-1$  C/100 m) and this layer is considered unstable (Blair and Fite, 1965). The depth of the unstable sublayer





Figure 4. Solar Elevation, Radiation Climate, and Temperature of the Air.

Curve 1. Solar altitude at Lake Hazen at 12:00 EST throughout the year (Corbet, 1966a).

Curve 2. Solar altitude at 24:00 EST throughout the year (Corbet, 1966a).

Curve 3. Ten day running means of mean daily air temperature in Stevenson screen (Jackson, 1959).

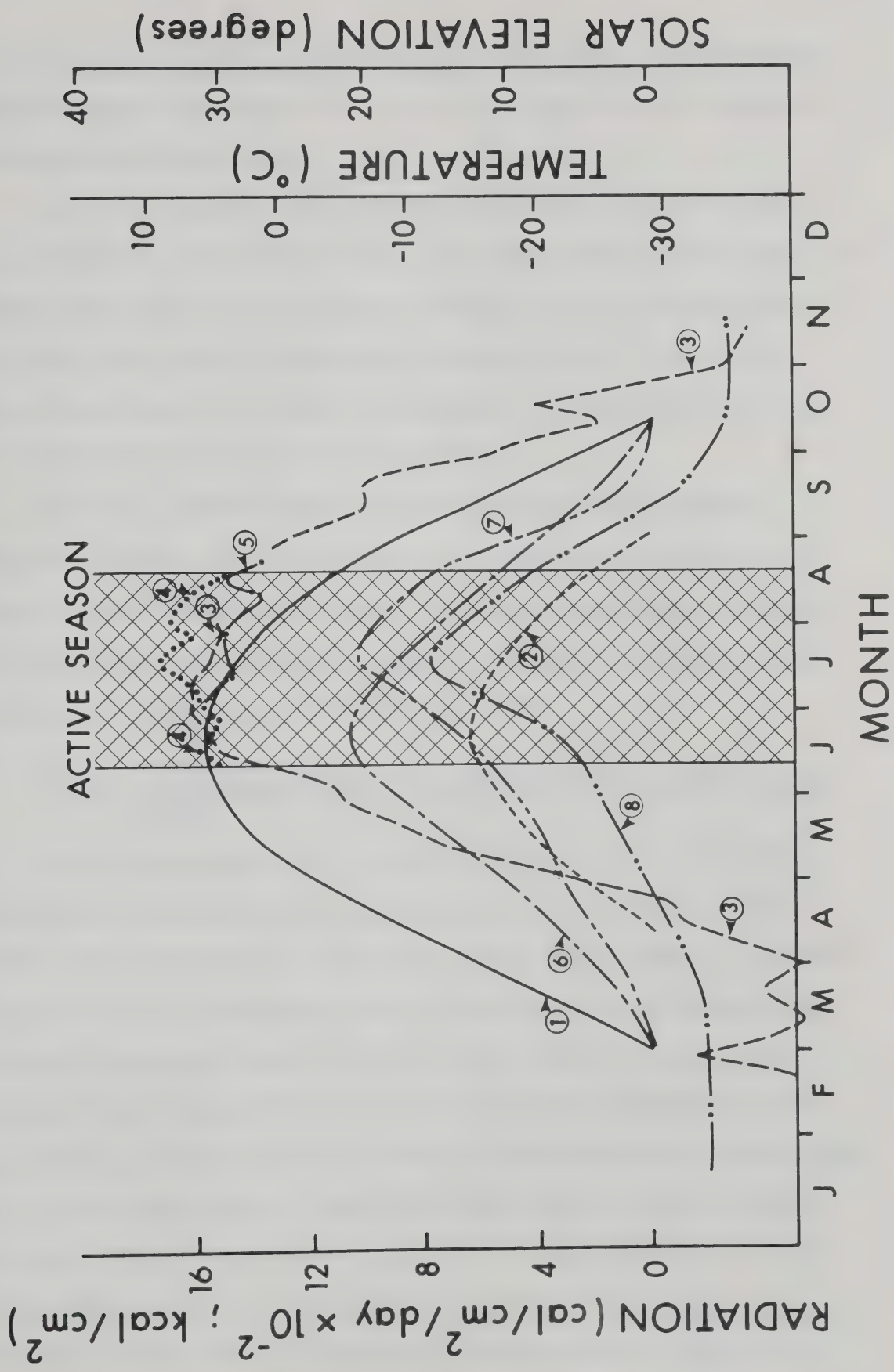
Curve 4. Seven day running means of mean daily air temperature in Stevenson screen during the warmest season, 1962 (Corbet, 1967a).

Curve 5. Seven day running means of mean daily air temperature in Stevenson screen during the coolest season, 1964 (Corbet, 1967a).

Curve 6. Undepleted solar radiation received on a horizontal surface at 80° N., cal/cm<sup>2</sup>/day (Gates, 1962; List, 1968).

Curve 7. Mean monthly absorbed radiation at Eureka Sound, kcal/cm<sup>2</sup> (Gavrilova, 1963).

Curve 8. Mean monthly radiation balance at Eureka Sound, kcal/cm<sup>2</sup> (Gavrilova, 1963).







varies with the locality, height of vegetation, etc. In this unstable sublayer of 100 m (Geiger, 1965) are the greatest vertical changes in meteorological conditions.

Within the unstable sublayer, and the active layer of the soil, terrestrial life activities proceed; and some aquatic habitats have the temperatures controlled by radiative warming of the substrate over which the water flows. Ultimately, therefore we must look to the radiation climate of an area to investigate its microclimate, which in part determines what sort of life occurs.

There has, however, been little comprehensive work linking radiation climate with microclimate, let alone with the biology of an area. The arctic, with its simple, almost two dimensional space (as opposed to the three dimensional space of forests) and limited biota presents an admirable locale for studying this.

#### I.5.6.1. Micrometeorology in the arctic, with reference to Hazen Camp

It has been realized for a long time that Stevenson screen air temperature measurements are inadequate when considering plant and insect life in the arctic, as is explained by Powell (1961). Although some of the early naturalists took spot readings of air temperatures close to the ground (Hartz, 1895; Lundager, 1917) it was not until Sørensen (1941) examined the phenology of northeast Greenland plants in relation to temperature that regular micrometeorological observations in the arctic were taken. Since then other work has been carried out by Bocher (1949), Bliss (1956), Mather and Thornthwaite (1956, 1958), and a number of Russian investigators (see Tikhomirov, 1963). At Hazen Camp, Powell (1961) carried out extensive work in relation to



the flora, and Corbet (1966a,b,c, 1967b, 1969) in relation to diel periodicities.

The tautochrones presented by Powell (1961) and Corbet (1967b) are similar and are of the incoming radiation type (Geiger, 1965) during the "active season". They showed that the first 10 to 20 cm have the steepest vertical gradient of temperature, and Corbet (1967b) demonstrated that the first 5 cm contributes most to the gradient in this layer, within which air temperatures may be as much as 8 C warmer than recorded in a Stevenson screen. During cloudy weather temperature gradients are much shallower as would be expected under conditions of reduced radiation (Geiger, 1965). In fact some of my observations show soil temperatures to be as low as or lower than the air temperature at 2 m. So it is not surprising that the zone from the soil surface up to about 20 cm embraces most terrestrial life, and insect activity is dependent on insolation and almost restricted to sunny weather.

Around Lake Hazen the low wind speeds, reducing the amount of turbulent mixing, result in shallower temperature gradients than elsewhere by allowing the warmed air to rise higher without cooling. Savile (1964) cites circumstantial evidence to substantiate this. Evaporative cooling is less important than in other arctic regions because of the low precipitation. Jackson (1959) showed Lake Hazen to have comparatively low relative humidities (sometimes less than 50%), and attributes this to strong insolational heating. Powell's (1961) data show decreases in relative humidity close to the ground, probably due to the same effects.

Corbet (1969) attributes the amelioration of microclimate in high latitudes to continuous daylight and the almost complete absence of



"nocturnal" temperature inversions.

#### I.5.6.2. Soil climate

Soil temperatures rise above freezing about three weeks prior to air temperatures in the Stevenson screen (Powell, 1961). The depth of unfrozen soil (the active layer) reaches a maximum of about 65 cm in late August (Yong *et al.*, 1962; Leech, 1966), but is greatly modified by plant cover and soil moisture from place to place (Powell, 1961).

Powell (1961) and Corbet (1957b) give vertical gradients of soil temperature and show that the soil surface temperature may be as much as 25 C warmer than the air temperature at about 2 m (Corbet, 1967b) and may reach 10 C at a depth of 30 cm (Powell, 1961).

#### I.5.6.3. Temperatures in ponds, tarns, and streams

Oliver and Corbet (1966) studied the temperature of various aquatic habitats in the Hazen Camp area. Generally the water temperatures are in excess of Stevenson screen air temperatures because of insolation warming of the substrate over which the water flows. The seasonal march of water temperature follows the march of air temperature.

#### I.5.6.4. Diel periodicities in microclimate

Corbet (1966a, 1967b) has shown diel periodicities in almost all weather factors during the "active season". He says:

"The diel fluctuation of solar altitude is sufficient to cause evident diel periodicities of light intensity, short wave radiation, screen air temperature, temperature at the surface of the soil and water, relative humidity and saturation deficit." (1966a)

Cloud cover causes these periodicities to become less evident; but





even cloud cover has a slight tendency to be less around solar noon, and this augments diel periodicities (Corbet, 1966a). The greatest diel range recorded by Corbet (1967b) at the soil surface was 20 C, but diel ranges are usually around 7 C (Powell, 1961).

Corbet (1967b) established that aspect also has an effect on microclimate and its diel periodicities. Diel temperature fluctuations are widest (and maxima greatest) on steep south or west facing slopes; i.e. slopes normal to the sun's rays at the warmest part of the day when the sun is highest, and shielded from the prevailing wind. There, the average diel range is about 22.5 C; even on the north facing side it is about 8 C.

These considerations have great bearing on very many aspects of insect life. Mosquitoes oviposit on the insulated side of moss hummocks (Corbet, 1964, 1966c), *Byrdia* caterpillars feed on the insulated side of hummocks, and butterflies bask on insulated slopes (Kevan and Shorthouse, 1970) as do mosquitoes and calliphorids. Savile (1964) recorded differences in the flora of south and north facing slopes, although these are not as pronounced in more southerly latitudes (Beschel, 1970).

#### I.6. Water Resources

There is very little summer precipitation in the Queen Elizabeth Islands because the lower troposphere is rarely close to saturation (Jackson, 1961a). Lotz and Sagar (1962) refer to northern Ellesmere Island as an arctic desert.

Winter snow contributes 2.0 inches of water, accounting for somewhat over 80% of the total precipitation (Jackson, 1959). Although the spring thaw of this snow offers the greatest supply of water, the



impermeability of the frozen ground lets it run directly off into the lake where it may flood the ice to a depth of 15 cm or more between Hazen Camp and John's Island. Some snow melt may be refrozen beneath the talus slopes of Mount McGill, to be released later in the season together with permafrost melt water.

Because of the above, and the low summer rainfall, the higher land is drained almost dry, remains arid and is sparsely vegetated. Low lying areas collect some of the spring melt in tarns and ponds, from which intermittent streams flow. It is in such drainage systems that most of the biomass is found, especially in wide sedgy areas. Melting snow and permafrost also contribute moisture to very hummocky areas at the bases of hills and hillocks where snow accumulates. Here again the luxuriance of the plants is greater than elsewhere.

Glacial melt water usually flows fast in shallow bouldery streams, often in the bottoms of ravines. Such river beds are intermittently inundated, as are the extensive outwash plains and deltas beyond. Neither of these habitats supports much life, except where soil has accumulated sufficiently to avoid inundation, or where there is soil on the banks or islands of the rivers. The flora in these two situations is different (*cf.* Savile, 1964), and quite rich.

The desert conditions of the Hazen Camp area are aggravated by the nature of water run-off. The result is a highly irregular distribution of life, which reflects the availability of water in 'oases' throughout the "active season."

### I.7. Conclusions

The Lake Hazen area enjoys a milder climate than does many arctic localities. This results from a combination of climate, particularly



high insolation and little cloud; and geographical location, in its being protected from high winds by the mountain chains to the north and northeast. The thermal stability, and low winds and lack of temperature inversions make for little turbulence close to the ground, and permit the development of a greatly ameliorated microclimate. The aridity reduces evaporative cooling, further contributing to the warmth of the environment.

Such apparent benevolence is not without its shortcomings. The place is a desert; observations on precipitation belie the availability of water, which determines the distribution of life. The richness of the flora can be attributed to mildness of climate and diversity of habitats, but aridity limits the biomass on land (Savile, 1964).

Areas of particularly favorable microclimate and water availability are the scenes of most insect activity, including flower visiting, and deserve greater attention than they have so far received.





## PART II

### BIOTIC ENVIRONMENT

#### II.1. *The Arctic Flora and its Adaptations, in Reference to the Hazen Camp Area*

The adaptations and ecology of arctic and alpine plants have been discussed by Bliss (1962a) and Billings and Mooney (1968). Tundra plants are characteristically dwarfs and grow slowly. In the arctic mortality of young plants is high (Wager, 1938). Almost all are perennials as the short summers do not allow completion of annual life cycles (Porsild, 1951). Of Raunkiaer's (1934) life forms chamaephytes, hemicryptophytes, and geophytes are the dominant forms in the Lake Hazen area as well as in the rest of the arctic (Powell, 1961). Among the chamaephytes are cushion rosette forms. These are especially well constructed for absorbing solar radiation, and regenerating as soon as the snow has left the ground, a phenomenon which is well documented by Wilson (1957), Tikhomirov *et al.* (1960), Tikhomirov (1963), and Bliss (1956). The last author comments on parallel evolution in the rosette form in a number of unrelated genera in relation to microclimate. Caespitose plants are better at resisting the effects of wind, such as desiccation and pruning (Hopkins and Sigafos, 1950; Wilson, 1959), although around Lake Hazen low wind speeds probably lessen the importance of this.

Many arctic plants appear to be xerophytes, having small leaves with thick cuticle or dense pubescence or both. Although the high arctic is very arid, many plants do not grow in areas where water is scarce. In fact, most grow where there is abundant water. Therefore thick cuticle and dense pubescence may be adaptations to freezing and



cold respectively. The thicker the cuticle and cell wall, the less likely are ice crystals, formed when the plant freezes, to puncture the cell walls and cause irreparable damage. Pubescence is significant in favouring radiative warming of some plants (cf. Tikhomirov *et al.*, 1960; Krog, 1955) and allows the leaves to thaw and mobilise their stored nutrients to begin development before the roots become active. This is, in part born out by the results of Billings and Bliss (1959) and Porsild (1951). Freezing tolerance is well demonstrated by Porsild's (1951) observations on the freezing and subsequent revival of *Salix richardsonii* and *Epilobium latifolium* over a short period of time. At Hazen Camp all plants must overwinter in the frozen state as soil temperatures below -40 C are known to occur (Powell, 1961). Desiccation may play an important role in the overwintering of arctic plants, and is reflected in the high osmotic values of the sap (Wager and Wager, 1938). Some species of far northern arctic plants, such as *Saxifraga oppositifolia*, may overwinter with the flower buds in a very advanced stage of development, and some may take two years to develop (Sørensen, 1941). *Braya humilis* is unique in that it can overwinter in any stage of its life (Sørensen, 1941).

It does not seem necessary for the roots of some plants to thaw before translocation occurs (Porsild, 1951). Roots of arctic plants are generally confined to the warmer and better drained layers of soil above the permafrost (Bliss, 1956). They are known to start metabolizing at between 0 C and 1 C (Bliss, 1956), that is soon after the snow has left the ground and well before screen temperatures have risen above freezing. Higher osmotic pressures in arctic plants (Wager and Wager, 1938) can be explained by cold, freezing resistance, desiccation, and



high osmotic pressures in the water in the soil (*cf.* Dadykin, 1964).

As might be expected from the micrometeorological studies growth starts just above and just below the soil surface almost immediately after snow has left the ground. The initial burst of growth is at the expense of stored carbohydrate reserves laid down the season before (Billings and Bliss, 1959).

In reviews Bliss (1962a) and Billings and Mooney (1968) discuss the data available on plant metabolism under arctic conditions. Respiration rates are higher than in temperate species at the same temperatures, and there is evidence that arctic-alpine plants are able to assimilate  $\text{CO}_2$  more efficiently and at lower concentrations (Billings *et al.*, 1966). Even so net assimilation rates are much lower than those reported for more temperate conditions (Wilson, 1960). Light saturation for photosynthesis too is lower in the arctic, lying between 5 and 20 kilolux (i.e. between 1.05 and  $9.0 \times 10^{-4}$  cal/cm<sup>2</sup>/sec\*) (Muller, 1928; Wager, 1941; Mooney and Billings, 1961). Annual plant production seems to lie between 3 g/m<sup>2</sup> to 224 g/m<sup>2</sup> depending on locality, plant community, grazing by animals, and sampling methods (Bliss, 1962c, 1970). No data are available for the caloric values of arctic ecological materials, but Mount Washington plants have high values linked with high lipid concentrations (Bliss, 1962b); it is not unreasonable to suppose that this may also be true of the arctic vegetation. High lipid and carbohydrate concentrations in plant cells, together with high osmotic values and greater sap concentration, must aid in cold tolerance in two ways;

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\* Calculated from List (1968) considering luminous efficiency at 680 lumens per watt.





one much the same as glycerol may help overwintering insects (Salt, 1961), and the other in easing water uptake (Dadykin, 1964). High caloric values must be of considerable importance to the nutrition of arctic herbivores, especially in winter.

Seed production may not be an important factor in reproduction of arctic plants as many of their seeds are inviable, according to Sørensen (1941) and Bliss (1958). This, however, is open to doubt as Savile (1964) reports that some 30% of the species of seeds collected from the Hazen Camp area have been germinated; and as Bliss (1958) points out the needs for germination are variable, leaving experimenters unsure of whether they have provided the correct conditions. Local microenvironmental differences influence flowering intensity and seed set (Bliss, 1956) and pollination, all of which decrease with severity.

Reproduction in many plants is completely apomictic, with the production of vegetative propagules. Apomixis may be the result of polyploid formation, and the propagated break-down of normal diploid sexual mechanisms (Gustavson, 1948). Hagerup (1932), Löve and Löve (1957), Johnson and Packer (1965), Packer (1969) have upheld various reasons for polyploidy being higher in the arctic than elsewhere. In the Lake Hazen area 65.5% of the dicots and 91.0% of the monocots are polyploid (Packer, 1969). Stebbins (1950) mentions the wider tolerance limits of polyploids for invading new habitats, the colonization of which would be accelerated by populations of genetically similar apomictic individuals. Löve and Löve (1949) attribute much of the success of arctic polyploids to their genetic superiority. Mosquin (1966) states that polyploids promote and preserve phenotypic uniformity in populations and resist natural selection on particular alleles. This may be important in



combatting alternations in the severity of the arctic environment over numbers of years.

All the above ideas point to the greater suitability of polyploid species for the arctic. However, it is interesting that some of the plants found under the most severe conditions are diploids such as *Silene acaulis*, *Oxyria digyna*, and *Saxifraga oppositifolia* (Bliss, 1962). Sokolovskaya and Strelkova (1960) regard diploids as part of the ancient arcto-alpine flora which may have resisted adverse conditions during the ice ages, while polyploids have moved into the arctic since the retreat of the ice. Savile (1964) concludes from the Lake Hazen area that many plants must have been widely distributed during the postglacial hypsithermal, and have subsequently become localized in valleys and fiords with mild summer climates.

#### II.1.1. Arctic Flowers and Adaptations to Pollination

The intense colours and large size of arctic flowers in proportion to the size of the plants has excited curiosity since the early days of arctic natural history (Bonnier and Flahault, 1878; Grisebach, 1877-1878; Aurivillius, 1883; Kjellman, 1883; and others). Grisebach attributed the above to the attraction of sparsely distributed insects while others denied this. Smell has been variously reported for arctic plants (Fridolin, 1936; Ekstam, 1895, 1897; Mosquin and Martin, 1967; Tikhomirov, 1959, 1963; and others). Nectar secretion by arctic plants has been shown to be more concentrated, and there may be  $3\frac{1}{2}$  times as much sugar produced per acre per season as in the forest at Churchill, Manitoba (Hocking, 1953). Intrafloral temperatures have been briefly examined by Krog (1955), Tikhomirov *et al.* (1960), Hocking and Sharplin (1965), Shamurin (1966b), and Hocking (1968). Elevated temperatures in



flowers may be of great importance to pollen tube growth, fertilization, and possibly seed development, as well as having a bearing on insect life. Pollen availability has not been considered in detail although Warming and others\* (1908-1921) mention the presence or absence of pollen in many of the plants they discuss.

Despite numerous devices in many flowers believed to attract insects, insect pollination of arctic plants is considered of little importance (Love, 1959; Mosquin, 1966) and the latter author states

"Thus although many arctic insects clearly depend on nectar- and pollen-producing, showy-flowered plants for survival, these plants may have little or no need for insects." p. 60

It is a well known fact that dichogamy is weakly developed in arctic plants (Warming and others\*\*, 1908-1921), while heterostyly is rare or unknown and the number of species of monoecious plants decreases with increasing latitude (Mosquin, 1966) (only one, *Salix arctica*, occurs at Hazen Camp). Mosquin links this with the breakdown of incompatibility mechanisms, and the increase in polyploidy allowing the invasion of high latitudes by many families.

Bliss (1962) maintains that self pollination is the most important mechanism for assuring seed set, while cross pollination helps gene flow and population diversity. Even so, Gavrilyuk (1961, 1966) reports that some 20 plant species in Chukotka are dependent on bees for pollination, and Shamurin (1958, 1966a,b) and Chernov (1966) report on great pollination activity by bumblebees and flies. The former author (1966b) records some plants dependent on insects for propagation (e.g.

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\* Meddelelser om Grønland, vols. 36 and 37.

\*\* Ibid.





*Astragalus alpinus*). More remarkable still is the co-distribution of certain legumes and bumblebees (Panfilov *et al.*, 1960; Chernov, 1966; Shamurin, 1966b).

#### II.1.2. The Flora of the Hazen Camp Area

Floral lists have been published by Powell (1961) and Savile (1964) and differ only in minor respects. Brassard and Longton (1969) provide some additional records. A list of dicotyledons, summarizing the above lists is given in Appendix I. I have followed the nomenclature of Porsild (1964).

#### II.1.3. Plant Ecology in the Lake Hazen Area

Plant associations in the arctic have been studied by Polunin (1948), Aleksandrova (Alexandrova) (1960, 1970), Beschel (1969, 1970), and many others, at Lake Hazen by Savile (1964), and at Tanquary Fiord by Brassard (1968).

Savile (1964) lists 12 principal habitats, and discusses the plants associated with each. The habitats are 'sand', 'gravel', 'clay plains and slopes', 'saline clay', '*Dryas* hummocks', '*Dryas-Kobresia* tundra', '*Dryas-Salix* tundra', 'muddy delta', 'gravel delta', 'boulder talus', 'springy slopes', and 'marshes and sedge meadows'. The communities associated with the last two listed, *Dryas* hummocks, and gravel are the most interesting in this study as they support large populations of entomophilous flowers. Figure 3 shows the distribution of the various habitats around Hazen Camp.

Around Gilman Camp one other community is evident, '*Arnica*-clay slopes'. Fields of the entomophilous *Arnica alpina* bloom in late July along the dry rivulet courses over clay slopes and plains. Tanquary



Fiord habitats are very similar to those around Hazen Camp, except for a few strand influences.

## II.2. Adaptations of Arctic Insects in Relation to the Hazen Camp Area

The adaptations of arctic insects have recently been discussed in detail by Downes (1962, 1964, 1965). He says (1964)

"It seems, however, that although the climate in the arctic is indeed severe, the severities as experienced by insects are not always of a random and catastrophic nature, but rather such as can be met more or less precisely by a particular constitutional adjustment,..."  
p. 301.

The overriding constitutional adjustment is in the maintenance of sufficient activity through adaptations for survival in environments of low heat budget. Bertram (1935) showed that this activity started at lower body temperatures. This is brought about in part by increased metabolism, (Bullock, 1955); and it is possible that different enzyme systems come into play at lower temperatures (Salt, 1961). The maintenance of activity is aided by structural and behavioral adaptations. Hairiness is greater in some arctic forms (Freeman, 1958) and this conserves metabolic heat (Church, 1960) as well as increasing and conserving absorbed solar energy (Krog, 1955). Melanism too is greater in arctic insects (Downes, 1962, 1964; Rapoport, 1969) and increases insolational heat gains (as well as radiation losses) (Gunn, 1942; Parry, 1951; Digby, 1955). Behavioral adaptations include basking in direct sunlight and exploiting favorable microclimates for a variety of life functions (Haufe, 1957; Hocking and Sharplin, 1965; Corbet, 1964, 1966b; Kevan and Shorthouse, 1970).

To facilitate the maintenance of activity throughout the continuous daylight circadian rhythms of more temperate insects have been replaced



by more versatile and opportunistic responses to prevailing wind and heat conditions. Diel periodicities of activity are well known in the arctic, but are correlated with diel periodicities in weather factors, rather than with endogenous rhythms (Corbet, 1964, 1965, 1966b, 1967c; Oliver, 1968; Syrjämäki, 1968).

Even though arctic insects exploit the environmental heat efficiently, and are active at low temperatures, the general level of insect activity throughout the short "active season" is considerably lower than in more southerly latitudes (Downes, 1965). Hence, some insects have extended and indeterminate life cycles (Aurivillius, 1883; Downes, 1964, 1965).

Overwintering by northern insects has been reviewed by Salt (1961), Sømme (1964), and others. Dehydration, glycerol, and ice crystal size and nucleation sites all play a role in permitting arctic insects to freeze in the winter, as they surely must overwinter in the first few inches of soil in areas of light snow cover, or in the open, or in tufts of vegetation where Johansen (1911) found frozen caterpillars of *Anarta* sp. Aquatic insects and larvae which overwinter in ponds that do not freeze to the bottom do not have the above problems (Oliver, 1964, 1968).

The obligate winter diapause, and emergence therefrom, serve to synchronize the appearance of adult insects after asynchrony resulting from the variation in life cycles (Downes, 1964). Most arctic insects emerge early as they are derived from groups which mature in the spring in temperate latitudes (Downes, 1962; Oliver, 1968). A few mature late and may oviposit parthenogenetically (*Apatania zonella*) or hibernate immediately (*Rhyngaenus* sp., *Bombus* spp. queens). Declining temperature may be the cue eliciting diapause which starts well before temperatures





drop too low for activity (Downes, 1965).

Flying is difficult for insects because of the cold, and because vegetation is too low to act as a wind break and insulation cover above flight height. Thus in some insects activities normally associated with flight, such as mating and feeding, are performed on the ground, or not at all; and accompanying this are corresponding changes in morphology and behaviour (Downes, 1965). Despite this strong fliers are well represented in the arctic (Downes, 1965; Oliver, 1963). At Hazen Camp I observed that flight heights rarely exceeded 5 m, and in general, were less than 0.5 m, as was demonstrated for butterflies by Kevan and Shorthouse (1970), that is within the region of greatest microclimatic amelioration.

#### II.2.1. Insect Fauna of Hazen Camp

Entomology in the Hazen Camp area dates from 1961 (Hattersley-Smith, 1962; Oliver *et al.*, 1964). Until 1966 the research program was run by the Canada Department of Agriculture (Hattersley-Smith and Oliver, 1967) and thereafter by the University of Alberta Department of Entomology.

Although Greely (1888) mentioned butterflies, Diptera, and bumblebees, previous to 1961 only three species of insects had been collected from Lake Hazen (Oliver, 1963): *Protophormia terraenovae* (R.D.) and *Fucellia pictipennis* Becker by Aldrich (1918), and *Pseudodiamesa arctica* Mall by Oliver (1959). Collections from the Queen Elizabeth Islands generally are recorded by McLachlan (1879), Kieffer (1926), Bruggeman (1958), and from the northwestern islands by McAlpine (1964, 1965a). Oliver (1963) provided a preliminary list of the insects of the Hazen Camp



area (including 189 species of Insecta, 14 species of Collembola, and 11 species of Arachnida) which he admits is incomplete. Newer lists are available for the Araneida, 13 species (Leech, 1966), and the Lepidoptera (Downes, 1966).

Fortunately most flower visiting species are fairly large and are included in Oliver's (1963) list, greatly facilitating identification.

### II.3. Interspecific Interactions: Food and Competition

The number of species of insects declines more rapidly to the north than that of plants, and within insects certain groups decline faster than others. The ratio of phytophagous insects to vascular plants goes from a 4:1 in Britain to 1:2.5 at Lake Hazen and 1:48 at Isachsen (extrapolated from Downes, 1964). This is due to environmental severity and independent of ecological interactions and limitations on food supplies (Downes, 1964).

Little is known of the feeding habits of many of the species at Lake Hazen. Some adult insects do not feed at all, some are quite specific in their food requirements, while others are broader in this respect than their temperate counterparts; examples of all the above are given by Downes (1962, 1964, 1965). Many insects in the Lake Hazen area are dependant on nectar no matter what other food supplies are used. For example the two species of mosquito (*Aedes nigripes* and *A. impiger*) are facultatively autogenous, and can mature a small number of eggs when fed only *Dryas integrifolia* nectar and denied blood (Corbet, 1964, 1967c). Nectar serves as the chief fuel for flight in arctic insects (Hocking, 1953, 1968).

Downes (1964) concludes that competition is at a low level and that diversification and speciation have not progressed far as a result



of the restrictions of the severity of the environment. Hocking (1968) states that insects do not compete for nectar.

The above discussion begs the question of biotic or ecological maturity, which are considered by Downes (1964) and Dunbar (1968) to be at a low level. Further clues to the level of maturity of high arctic ecosystems could be gained from examining the relative numbers of plants, herbivores, carnivores, sarcophages, and parasites, and especially the diversity within each of these groups in comparison with more mature ecosystems.

#### II.4. Conclusions

The biotic environment functions according to the opportunistic responses of both plants and insects; they tend to co-habit in localized areas of ameliorated microclimate. For both groups the major limiting factor of the biota is environmental severity, while the biomass is limited by the water availability to plants upon which animals are dependent, directly or indirectly for food.

Within the biologies of plants and insects are a number of paradoxes which may be explained by responses to environmental severity and immaturity of the ecosystem. In plants we find vegetative reproduction, facultative seed set, facultative pollination, and obligate pollination, in conjunction with diploidy and polyploidy; these phenomena are not entirely adequately explained by modern theories. In adult insects we see greater food diversity in some species to lack of feeding in others; aptery and stronger flight; wide and narrow behavioral patterns: simple parthenogenetic reproduction leading to genetic stability, and widely distributed variable species; low endemism; and low reproductive potentials (Downes, 1965) together with adaptations to the harsh





environment, which one might think would necessitate the opposite.



### PART III

#### INSECT-FLOWER RELATIONS: REVIEW

##### III.1.1. Insect-Flower Relations: General Review

The significance of insect visits to flowers was first realized in 1750 by Arthur Dobbs (Grant, 1949). K8lreuter (1761-1766) described the importance of these visits and is generally credited with the discovery of insect pollination. Since then there have been several monumental contributions by Sprengel (1793), Delpino (1867-1875), Hildebrand (1863-1902), M8ller (1873), Darwin (1876, 1882), and Knuth (1895-1902, 1906 -1909) which greatly expanded the study and laid the background for modern work. Experimental work started with Plateau (1876-1910) and really got underway with von Frisch (1914, 1919), Knoll (1921), and Clements and Long (1923). Some modern syntheses explaining the principles behind pollination are by Vogel (1954), and Meeuse (1962), Grant and Grant (1965), Percival (1965), Faegri and van der Pijl (1966), and Baker and Hurd (1968).

Angiosperms surged into importance in the late Cretaceous period, and were the dominant floras of all latitudes by the Tertiary period. One of the most characteristic features of the angiosperms is the adaptation of their flowers for pollination by animals, particularly insects. Some of the pollination mechanisms become exceedingly complex and precise as certain flowers co-evolved with particular insects (and *vice versa*) to ensure the carriage of the correct pollen to the correct stigma by a single species of insect, which alone is able to reap the benefits of visiting those flowers. The histories of the Angiosperms and Insecta in relation to one another is given by Leppik (1957b,



1963a), Baker and Hurd (1968), and from the point of view of the Angiosperms by Eames (1961) and Baker (1963).

Despite the wealth of information on the significance of insect-flower relationships to plants, their "significance to insects has been neglected" (Hocking, 1953). It is refreshing to see Elton (1966) devote a chapter, entitled "Natural Fuel Stations: Concourses on Flowers and Fruits" to this subject.

### III.1.2. Insect-Flower Relations in the Arctic: Review

Cursory observations were made by many of the early naturalists who visited the arctic (Holmgren, 1869; Lindman, 1887, 1888; Hartz, 1895; Deichman, 1896; Ekstam, 1894a,b, 1895, 1897; Warming, 1909; Nielsen, 1910; Johansen and Neilsen, 1910; and others). The first list of specific visitors to arctic flowers is given by Longstaff (1932) who discusses flower visitors in his general discussion of the ecology of west Greenland. Early records of arctic bumblebees and the flowers they visited are included in some of the above and dealt with specifically by Friese (1902, 1904, 1908), Schneider (1894, 1906), Frison (1919), Sladen (1919) and others (see Richards, 1970). Høeg (1924, 1929) carried out pollen analyses from arctic bumblebees, and added more cursory insect-flower associations in 1932.

After Aurivillius' (1883) expert treatment of insect life in the arctic in relation to the knowledge of pollination and the arctic flora, little comprehensive work was done. Fridolin (1936) appears to have been the first 20th century scientist to have tackled the problem systematically in his study of the plant and animal associations in the Khibini mountains.

In the U.S.S.R. the Komarov Botanical Institute in Leningrad has





been active in this field (Petrovskii, 1964). Shamurin (1956, 1958, 1960a,b, 1962, 1966a,b) reports on great pollination activity by numbers of insects, particularly flies and bumblebees from the Tiksi Bay region, and associates their visits with the phenologies of the flowers involved. Gavriilyuk (1961, 1966) mentions some 20 plants dependent on bumblebees for pollination in Chukotka. Panfilov *et al.* (1960) report on the joint occurrence of bumblebees and legumes throughout the Soviet arctic. Recently Chernov (1966) has considered the complex of anthophilous insects over the Soviet tundra based on his earlier works (1959, 1961, 1963), and on the afore-mentioned studies. Tikhomirov (1959, 1962, 1963) has shown particular interest in these developments.

In Canada entomologists interested in the livelihoods of arctic insects have investigated insect-flower relations. Hocking (1953), Hocking *et al.* (1950), Hocking and Pickering (1953), and Twinn (1952) have alluded to the importance of nectar as fuel for flight by subarctic biting flies. In the high arctic Oliver *et al.* (1964), and Downes (1964) remark on the multitude of visitors to flowers of *Dryas integrifolia*, and Corbet (1964) specifically mentions mosquitoes. Milliron and Oliver (1966) and Richards (1970) note some of the flowers visited by bumblebees. Papers dealing specifically with insect-flower relations are by McAlpine (1965b) on anthophilous Diptera, Kevan and Kevan (in press) on Collembola, Hocking and Sharplin (1965) on flower basking by arctic insects, Mosquin and Martin (1967) on general pollination biology, and Hocking (1968) with respect to nectar secretion by high arctic flowers.

From this background material there appear many gaps in our knowledge of the importance of insect visits to flowers, which Mosquin



(1966) feels are unimportant for pollination but which several Russian scientists have shown are entirely responsible for pollination in several plants (see above). The importance of flowers to the insects has also been insufficiently studied. Although nectar is vital for the existence of insects in the high arctic, nectar requirements have not been correlated with development and physiology. Pollen feeding has hardly been touched upon, except for isolated observations. No correlations of this protein uptake with physiology and development have been made. There is also confusion regarding the mechanisms by which arctic flowers attract insects.



## PART IV

### ARTHROPODS ON FLOWERS

#### IV.1. *Materials and Methods*

Between 25 May and 6 August 1967, over 2,500 observations were made of individual arthropods on flowers. Material from similar collections of 1966 and 1968 was not used unless otherwise stated. Only the material collected in 1967 has been examined completely. Every specimen was identified as far as possible, most to species, and all to family. Specific identifications were not always possible as some material is poorly known taxonomically, is undescribed, damaged, or was not collected. I used a pocket tape recorder (De Jur -- Grundig EN 3) with a lapel microphone to make running commentaries on the activity, position, and amount of pollen dusting of each specimen. This left both hands free for collecting and allowed continuous observations. The specimens collected were preserved in alcohol and examined in laboratories at Hazen Camp and at the University of Alberta. Pollen adhering to the cuticles and setae of the animals was noted. Most specimens were dissected, and the contents of their guts examined for pollen grains. At the same time the ovaries of the females were examined and the state of development of the most advanced follicle recorded on a scale of 4, which is compared in Table 1 with Christophers' stages of the ovarian development of mosquitoes as modified by Clements (1963: 173-174), and by Harlow (1956) for *Protophormia terraenovae* (R.D.).





Table 1.

Stages of ovarian follicular maturation with descriptive criteria, and compared with Christophers' (as modified by Clements (1963: 173-174)) and Harlow's (1956) stages.

Stage	Description	Christophers'			Harlow's	
		Stages			Stages	
1	follicles very small	Ia	Ib		1	2
2	follicles enlarging, trace of yolk	IIa	IIb		3	
3	follicles enlarging, yolk obvious, occupying from 1/10 to 9/10 of follicle	IIIa	IIIb	IVa	4	
4	follicle assumes the shape of mature egg, yolk occupying all the follicle	IVb	V		5	
spent	no follicles present all eggs laid					

All the information gathered on each specimen was punched onto analysis cards (Systems Equipment Ltd., Winnipeg. Std. Form Y 9) to facilitate the extraction of data.

#### IV.2. Acarina

Oliver (1963) lists only one mite, *Libertia* sp. (Hydracarina).

I found several species of mites on flowers around Hazen Camp. The most common were *Bryobia "praetiosa"* Koch (Tetranychidae)\* \*\*. I found these mites on several of the species of Cruciferae; *Lesquerella arctica* (2, 29.VI.1966; 52, 3.VII.1967; 7, #5.VII.1967; 2, 23.VII.1967), *Draba Bellii* (5, 26.VI.1966), *Erysimum Pallasii* (4.VII.1966),

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\* It is impossible to say if these are *B. praetiosa sensu strictu*. They belong to the *B. "praetiosa"* group (Kevan and Emberson, pers. comm.).

\*\* Those collected in 1966 were identified as *Bryobia* sp. by E.E. Lindquist.



many on *Draba cinerea*, *D. groenlandica*, *Braya humilis*, and others on 3.VII.1968; I also found them on *Papaver radicatum* (29.VI.1966), *Potentilla nivea* (3.VII.1967; 14.VII.1967), and *Dryas integrifolia* (2, 3.VII.1967 & 13.VII.1967). They feed on plant sap and were found generally over the plants as well as on the flowers. Other mites were collected from *Saxifraga oppositifolia*; they are *Arctoseius cetratus* (Sellnick) (Ascidae, Arctoseiinae) (5f, 3.VI; 1f, 7.VI; 1f, 8.VI.; 3f, 11.VI.1967), Eriophyidae, genus undet. (2, 7.VI.1967), and *Cecidophyes* sp. (Eriophyidae) (2f, 11.VI.1967). Those collected on *S. oppositifolia* were associated with chironomids *Smittia velutina* Lundbeck but this is probably incidental as the eriophyids are plant parasites and the ascid is a free living predator of nematodes and micro-arthropods (Lindquist, pers. comm.). I also collected some unidentified mites from staminate and pistillate *Salix arctica* catkins.

#### IV.3. Araneida

The only spiders regularly found in flowers are the Crab spiders (Thomisidae) (Gertsch, 1949). Leech (1966) has studied the spiders of the Hazen Camp area from 1963 and 1964 and describes the taxonomy, biogeography, and aspects of the life histories of 13 species of 4 families. I found 5 of these species, representing all families, in association with flowers.

##### IV.3.1. *Dictyna borealis* Pickard-Cambridge (Dictynidae)

Four specimens were collected in association with various flowers. On 8.VI.1967, 1 adult male was collected in a clump of *Saxifraga oppositifolia*; although it was not on the flowers, it was dusted with pollen. On 3.VII, 1 immature male was collected from a *Potentilla*



*nivea* flower, across which it had built a web from the petals of one side to the pistils. On 16.VII, 1 immature was taken in *Lesquerella arctica*; and on 18.VII, 1 penultimate male was collected on *Arnica alpina*. The latter three had no pollen visible on them. Hocking (1968) noted 1 on *Potentilla* (27.VII.1963) in ambush. Leech (1966) says that these spiders are most commonly found on *Dryas integrifolia* hummocks, but I did not find them in the flowers of this plant, although I recorded a dead female of *Spilogona melanosoma* Huck. from a web, probably of this spider, across a flower (5.VII.)

IV.3.2. *Pardosa glacialis* (Thorell) (Lycosidae)

Three immature and 1 adult male were collected in association with *Salix arctica* catkins between 8.VI and 10.VI.1967. None were dusted with pollen, although 1 was on a staminate catkin.\*

IV.3.3. *Tarentula expasperans* Pickard-Cambridge (Lycosidae)

I found two immature specimens, one female, in clumps of *Saxifraga oppositifolia* on 8.VI.1967; neither carried pollen. Although these were not within the flowers, I assumed that they were using the site for capturing prey in much the same way as does *Scatophaga apicaulis*. One specimen, lost in transit, probably of this species was found on 7.VI on a *S. oppositifolia* flower eating a specimen of *Phalacrodira nigropilosa*.

IV.3.4. *Erigone psychrophila* Thorell (Linyphiidae)

On 3.VII.1967, 1 adult female of this small spider was found under the filaments of a flower of *Dryas integrifolia*. It was dusted with pollen.

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\* The sex of the catkins was not recorded for the others.





IV.3.5. *Xysticus deichmanni* Soerensen (Thomisidae)

Between 10.VI.1967 and 21.VII.1967, 52 specimens of this spider were collected or observed or both from flowers of 5 species. The first records were 2 immature specimens collected on 10.VI from *Saxifraga oppositifolia* and *Erysimum Pallasii*; and 2 immature females, 1 on *S. oppositifolia* (10.VI) and 1 on *Dryas integrifolia* (28.VI). Only the last specimen carried pollen; very few grains on one leg. I collected one other immature female later in the season (18.VII) from *Arnica alpina* at Gilman Camp, its venter was dusted with pollen. Three penultimate females were collected; 1 on a staminate catkin of *Salix arctica* (10.VI) with pollen dusted on its palps, chelicerae, and legs; 2 on *D. integrifolia* (10.VI and 13.VII) which were not dusted with pollen. The gynoeceum of the flower in which the latter rested had been partially eaten by a larva of *Sympistris labradoris*, but there was no sign of the caterpillar, which may have been eaten (cf. Leech, 1966; Hocking, 1968). Eight penultimate males were taken, two were found on the shaded side of staminate catkins of *Salix arctica*, one with a little pollen on its palps (10.VI). Three were taken from *S. oppositifolia* (10.VI), one had a cache of 2 Syrphidae (male *Carposcalis carinata*) lying dead and sucked dry beneath the flower, neither of these flies was dusted with pollen. On 16.VII, 1 was collected on *D. integrifolia*, it was dusted with pollen on its legs and had a few grains on its palps. One other was taken on *A. alpina* (17.VII), its venter, legs, and palpi were dusted. The last 2 were from Gilman Camp. No adult males were collected from flowers, although they are abundant (see Leech, 1966). Seven adult females were collected; 2 waiting on the shaded side of staminate catkins of *S. arctica* (10.VI), both had



pollen on their palpi; 5 were taken on *D. integrifolia* (1, 28.VI; 2, 13.VII; 2, 17.VII (1 at Gilman Camp)), 2 had prey, 1 an ichneumonid *Mesoleius* sp. and the other with 2 dead insects (Muscidae and *Spilogona* sp. 17.VII). All these had pollen on their feet, except one which was captured as it climbed the stem of a flower.

Three individuals were observed on *D. integrifolia* (9.VII-15.VII) but not collected, similarly 28 were recorded from *A. alpina* at Gilman Camp (15.VII-21.VII), of which 1 was preying on *Rhamphomyia* sp. In 1968 I collected specimens from the flowers of *Lesquerella arctica*, and *Erysimum Pallasii* as well as from some of those mentioned above.

Leech (1966) remarks that both he and Oliver found specimens hiding in *D. integrifolia* flowers, presumably waiting to catch visiting insects. All the observations I made were of spiders in the typical ambush position. Hocking (1968) records the same thing, for 2 immature specimens (my inference) in *D. integrifolia* and 5 adult females in various flowers (2 in *D. integrifolia*, 1 with *R. filicauda* as prey; 1 in *Papaver radicum*; and 2 in *A. alpina*.

The spiders on the flowers of *S. oppositifolia* and *E. Pallasii* had a distinct purplish tinge in comparison with those from yellow flowers. Perhaps these spiders\* can assume cryptic colouration according to their background as is recorded by Wickler (1968: 54) for *Misumena vatia* (Clerck) (Thomisidae). I found that these spiders do not reflect ultraviolet (at least on an ultraviolet absorbing background). All 28 specimens observed on *A. alpina* were at the proximal ends of the ray florets, or on the disc where there is no ultraviolet reflection,

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\* Trapped specimens of *X. deichmanni* differ from one another in colour (Leech, pers. comm.).



hence they are less visible to insects. Eisner *et al.* (1969) however, found the ultraviolet reflecting spider *Misumenoides formosipes*\* (Thomisidae) on the ultraviolet absorbing disc of *Viguiera dentata* (Compositae).

Except for adult males, all stages of this spider are carnivorous. Thus all stages, but adult males and those too small to attack most anthophilous insects were encountered waiting in ambush in flowers.

#### IV.4. Collembola

Collembola have only rarely been recorded in flowers (Kevan and Kevan, in press) and in the arctic only by Hocking (1968). The Collembola of the Hazen Camp area are incompletely known.

##### IV.4.1. Entomobrya comparata Folsom

Twenty observations were made on these animals. On 3.VII.1967, 6 specimens were collected from deep in the corollas at the base of the gynoeceum and near the nectaries at the bases of the petals of *Lesquerella arctica*. Five were taken along the lake shore at L 13, and one other along the west bank of Blister Creek in C 14. No further collection or observation was made despite searching, until 16.VII, when two specimens were collected in exactly the same circumstances in the same species of flower along the lake shore a little to the west of Gilman Camp. Exactly 1 year later (3.VII.1968) 2 specimens were observed and photographed on one plant, but on separate flowers of *L. arctica*. They were watched through a 20X hand lens as they appeared to feed directly from the dehiscent anthers of the flowers. Each was observed

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\* = *Thomisus formosipes* Walckenaer ?, species name in question (Leech, pers. comm.).





within the same flower for more than 15 minutes, during which time they moved about on the anthers. One moved from one anther to another in the same flower, crawling down the filament of the one, and up onto the anther of the adjacent stamen. Whilst on the anthers the postures of these animals did not change. They held on with all 6 feet, their abdomens curled loosely over the surface of the anther, but not appressed to it. They continually waved their antennae, again curved over the surface of the anther, which they frequently touched. Their mouthparts were seen to be applied to the surface of the anther, and it was assumed that they were eating pollen. One other specimen was collected from *L. arctica* that day in the same area. The next day, 4.VII., 1 specimen was observed in a flower at T 3, but it escaped. On 5.VII, 6 specimens were collected and 2 more closely observed, but others seen in various parts of the Hazen Camp study area escaped. Of the 6 collected, 3 were taken on the same *L. arctica* plant, and 2 within the same flower. The 2 which were closely observed behaved exactly as is described above for those eating pollen.

15 specimens were sent to the Lyman Entomological Museum, McGill University, for identification by Mr. K. P. Butler. He examined them for pollen grains within their guts. Every specimen had ingested the spherical pollen grains whole (*cf.* Scott and Stojanovitch, 1963). Presumably digestion is by diffusion through the micropylar membranes, as in bee larvae (Whitcomb and Wilson, 1929; Faegri, 1962), Syrphidae (Müller, 1873; and below), *Pogonomyoides segnis* (below), and most other Collembola (Kevan and Kevan, in press).

So far this animal has been found only on *L. arctica*. Its activity on these flowers appears to be limited to a very short period (1 day



in 1967; 3 days in 1968) although the flowers persist well over 1 month. I think that this activity can be regarded as occurring in a "sensitive period" of their life cycle. Shelford (1963: 8-9) writes: "Sensitive periods sometime last only a few days and may be difficult to detect. However, the identification of these sensitive periods in the life cycles of both plants and animals is very important for understanding their distribution, seasonal occurrence, and abundance." He also writes "The activity or vital process which takes place within the narrowest environmental limits is usually the most important ecological feature of a life cycle." Thus the activity of these animals within the flowers of *L. arctica* may be important to some aspect of their life history, perhaps to egg maturation. It is possible that some of the specimens were feeding on nectar as well, the sugars of which would provide fuel for prolonged activity. Collembola have never been reported to feed on nectar, but the fact that some of those collected were near the nectaries opens this possibility.

#### IV.4.2. Other Collembola

On 16.VI.1968 a single unidentified dark specimen was collected from the corolla of *Saxifraga oppositifolia*. Hocking (1968) records Collembola sp. from *Cerastium arcticum* and *Isotoma viridis* (Bourlet) from *Saxifraga Hirculus*.

#### IV.5. Homoptera, Aphididae

No aphids were recorded from flowers. Hocking (1968) remarks on *Brevicoryne arctica* Richards on its host plant *Lesquerella arctica* from 16-22.VII.1963, but not specifically on the flowers. I noted this species on the leaves of *L. arctica*, but never found them on the



flowers. A similar relationship could also be claimed for *Cavariella borealis* Hille Ris Lambers which was found on the leaves and petioles of *Salix arctica*, but never on the catkins. At Tanquary Fiord (17.VIII-22.VIII.1968) the population of this aphid was so high on *S. arctica* that the resulting honey-dew was dried on the pebbles and sand beneath the leaves, making them shiny and sweet to taste. Many syrphid larvae were preying on these aphids, but nothing appeared to be making use of the abundant honey-dew. The infestation extended several kilometers either side of Tanquary Fiord Camp.

#### IV.6. Coleoptera

I have no observations of anthophilous beetles at Hazen Camp, but Hocking (1968) records 1 individual of *Rhyncaenus* sp. (Curculionidae) hidden in a staminate catkin of *Salix arctica*.

#### IV.7. Trichoptera

Trichoptera are not known to be anthophilous. I made a single observation of the one species at Lake Hazen, *Apatania zonella* (Zetterstedt) resting on a petal of *Dryas integrifolia* on 16.VII.1967. Many specimens were seen flying along the lake shore that day.

#### IV.8. Lepidoptera

Downes (1966) recently examined the Lepidoptera of Greenland. He provides information on their zoogeographical affinities with the Canadian high arctic, augmenting the list of Oliver (1963). Lepidoptera are well known visitors to flowers.

##### IV.8.1. Geometridae

Two species of Geometridae are known from Hazen Camp, *Dasyuris*





(*Entephria*) *polata* Dup., and *Psychophora sabini* Kby (Oliver, 1963).

None were collected from flowers, although they probably feed on nectar.

#### IV.8.2. Lymantriidae

Two species of Lymantriidae are known from Hazen Camp, *Byrdia* (*Gynaephora*) *rossi* Curt. and *B. (G.) groenlandica* Hom. Despite the large numbers of larvae found, adults seem uncommon (cf. Oliver, 1963). None were collected in flowers, although they probably feed on nectar. Larvae were collected eating the inflorescences of *Salix arctica* (male) (14.VI.1967) and *Dryas integrifolia* (1966).

#### IV.8.3. Pterophoridae

One species of this family *Stenoptilia mengeli* Fern. is known from Ellesmere Island (Downes, 1966). None were collected from Hazen Camp in 1967. The larvae of some species are known to feed in flowers (Imms, 1964).

#### IV.8.4. Tortricidae (Olethreutidae)

There are 3 species of Tortricidae known from Hazen Camp, *Aphania* sp., *Olethreutes inquietana* Walk., and *O. mengelana* Fern. (Oliver, 1963; Downes, 1966). The Tortricidae are not well known flower visitors. Specimens of *Olethreutes inquietana* were collected at Hazen Camp in 1967 by J. Shorthouse, but only one male was found on an inflorescence of *Taraxacum arctogenum* on 2.VII; its activity was not ascertained. Hocking (1968) recorded 6 specimens of *O. inquietana* from *Dryas integrifolia*. He also recorded *O. mengelana* on *D. integrifolia* on several occasions, and once on a flower of *Potentilla* sp. The activities of all these are uncertain.



#### IV.8.5. Small Moths

The families Olethreutidae and Pterophoridae constitute the small moths at Hazen Camp. Four specimens of small moths were observed in flowers at Hazen Camp in 1967, but unfortunately escaped. They probably belonged to the genus *Olethreutes*. Two specimens were seen imbibing nectar from *T. arctogenum* with their probosces extended into the florets (8.VII & 17.VII). On 17.VII one specimen was observed imbibing nectar from *Potentilla* (prob. *nivea*).

#### IV.8.6. Arctiidae

Arctiid larvae have been found at Lake Hazen (Oliver, 1963; Downes, 1966) but no adults.

#### IV.8.7. Noctuidae

Five species of noctuids are known from Hazen Camp, *Anarta* (*Hadena*) *richardsoni* Curt., *Crymodes* (*Apamea*) (sp. nr.?) *exulis* Lef., *Lasiestra leucocycle* Staud., *Sympistris labradoris* Staud., and *Syngrapha parilis* Hon. (Oliver, 1963; Downes, 1966). Noctuidae are common visitors to flowers (cf. Müller, 1873, p. 467) as is true in the arctic.

##### IV.8.7.1 *Anarta* (*Hadena*) *richardsoni* Curt.

Thirteen specimens were collected or observed on flowers in 1967. On 2.VII, 1 specimen was observed on a staminate catkin of *Salix arctica* resting vertically, head uppermost. Three males (10.VII; 13.VII; Gilman 16.VII) were collected from *Dryas integrifolia*, two imbibing nectar, the third resting; all were dusted with pollen. I watched as one specimen approached a flower; it flew from behind the flower, landed on it and crawled over onto the front where it



probed its tongue between the stamens and pistils while gripping the edges of the petals with its meso- and meta-tarsi. Six other specimens were observed on *D. integrifolia*, but escaped; 2 were seen as they hovered in front of flowers before landing and assuming a position similar to the above to feed (26.VI). 1 specimen was observed on a flower of *D. integrifolia*, but its activity was not ascertained (4.VII); 3 specimens were seen imbibing *D. integrifolia* nectar (5.VII), 1 of them was observed as it landed on the lower petals of the flower, it then pulled itself up so that its thorax lay across the pistils and its tongue could be inserted into the nectar, it then began to feed. I watched one male as it approached a bloom of *Arnica alpina* (Gilman 14.VII); it flew towards the center of the flower, but blown by a gust of wind, missed its landing. I could find no pollen on its body. On 19.VII a male and another individual were observed imbibing the nectar of *Polygonum viviparum*, the male was oriented vertically, with its head lowermost, it inserted its proboscis into several flowers. It carried no pollen. The only female collected (of 5 sexed specimens) was observed imbibing nectar from *Taraxacum* sp. (prob. *arctogenum*), it was oriented vertically, head uppermost, and there were a few pollen grains adhering to its body.

Hocking (1968) recorded 1 specimen with uncertain activity on *Saxifraga tricuspidata* and 2 specimens from *Dryas integrifolia* imbibing nectar.

The scarcity of females on flowers may be explained as that of *Crymodes* (*Apamea*) *exulis*.

Larvae were collected eating the inflorescences of *Salix arctica* (2, 3.VI; 3.VI; 2, 8.VI; 3.VI), and *Oxyria digyna* (17.VI, 11.VI).





IV.8.7.2. *Crymodes (Apamea) exulis* Lef.

Eleven specimens of this moth were collected from flowers. On 10.VII.1967, 2 males were collected as they imbibed nectar from *Dryas integrifolia* flowers, one was well dusted with pollen, while the other carried a few grains on its proboscis. On 13.VII a male was watched as it landed on *Arnica alpina*; as it landed on the ray florets of the lower half of the inflorescence it was blown off by a gust of wind, it re-approached the flower, landing on the lower ray florets from whence it crawled onto the disc and began feeding, walking around the disc inserting its proboscis into numerous disc florets. It was well dusted with pollen, under the thorax and between the coxae. On 18.VII a male was taken on *A. alpina*, its activity was not ascertained. It was dusted with pollen. On 20.VII, 5 males were collected from *A. alpina*, 4 of them carried pollen. The only female collected was taken from *A. alpina*, and had a few pollen grains dispersed over its body. On 19.VII a male was collected as it imbibed nectar from *Polygonum viviparum*, it was watched as it inserted its proboscis into several flowers. It carried no pollen. Hocking (1968) recorded one specimen of this moth on *Erysimum Pallasii*.

The scarcity of females on flowers (1 to 10 males) may well reflect their lesser need for fuel for flight, as the males search out the females for mating. Downes (1964) noted that the females of some species of arctic moths (e.g. *Psychophora sabini* and *Pachnobia* spp.) show varying degrees of brachyptery and are lethargic, being sought after by the normal winged active males. Reluctance or lack of need to fly may be the first stages of this syndrome and is reflected in the sparsity of females taking nectar as flight fuel (cf. *Lasiestra*



*leucocyla*).

IV.8.7.3. *Lasiestra leucocycla* Staud.

Fourteen specimens of this moth were collected from flowers in 1967. On 9.VII, 1 male was collected as it imbibed nectar of *Dryas integrifolia*, it had pollen on its venter and tongue. On each of 10.VII (Hazen Camp) and 13.VII (Gilman Camp), 1 female was collected in the same circumstances, the former had pollen on its eyes. On 16.VII, 2 specimens were seen on *D. integrifolia*; the one collected was male, it was observed as it approached the flower from behind and landed on the flower, gripping with its meso- and meta-tarsi, it then flapped its wings as it crawled over onto the front of the flower where it oriented itself horizontally and fed. After it had finished it merely dropped to the ground, rather than flying off. This specimen had pollen liberally dusted on its head and tongue. On 14.VII, at Gilman Camp, 2 males were collected from *Arnica alpina*. One was watched as it walked around the flowering head turning through 180° inserting its proboscis into the disc florets. Only one was dusted with pollen. At Gilman Camp, I watched a female approach a flower of *A. alpina* from behind as described above for *D. integrifolia* (16.VII) and begin feeding. It did not maintain any orientation, but rather walked around the flower probing into the disc florets with its tongue. It carried a little pollen. On 18.VII at Hazen Camp, 1 female was collected from *A. alpina*, it carried one or two pollen grains. On 19.VII, at Gilman Camp, 1 male with only 1 pollen grain detected on it, and 1 female dusted with pollen, were collected on *A. alpina*. On 21.VII at Gilman Camp 1 male and 2 females were collected from *A. alpina*, all carried pollen. On 19.VII, 1 female was collected as it



imbibed nectar from the apex of a *Polygonum viviparum* spike; it carried no pollen.

Hocking (1968) collected 2 specimens of this moth, 1 from each of *Lesquerella arctica* and *D. integrifolia*.

The sex ratio in this species is 6 males to 8 females, indicating that both sexes are active fliers (cf. *Anarta (Hadena) richardsoni* and *Crymodes (Apamea) exulis*).

#### IV.8.7.4. *Sympistris labradoris* Staud.

One adult male of this species was recorded from *Papaver radicum* on 6.VIII.1967. It appeared to be attempting to imbibe the nonexistent nectar; its tongue was lapping at the bases of the petals.

Hocking (1968) infers from the presence of first instar larvae in the corollas of *Dryas integrifolia* that females visit these flowers for oviposition. I collected several large larvae (4,20.VI; 2,18.VI; 1,12.VII; 2,20.VII.1967). I noted then that many of the flowers around were damaged, the gynoecium and androecium eaten out: nothing but frass remained in the corolla. I also noted that many buds had holes chewed through the unexpanded petals, often near the apex; the developing gynoecium and androecium were totally eaten, only larvae or frass or both left. From Hocking's (1968) data and the above it seems that the adult females oviposit in the flowers, or at least in association with the plants. The young larvae dine on the ovaries and stamens, presumably moving from flower to flower, developing until the blooms are no longer available. It seems that over-wintered larvae emerge as the flowers develop, and crawl up onto the buds, chew into them and resume feeding as previously. The number of cycles required for larvae development is unknown, and may well be variable (cf. Downes, 1965).





IV.8.7.5. *Syngrapha parilis* Hbn.

Neither adults nor larvae were collected in 1967 nor were they observed in association with flowers. These medium sized moths are likely to be flower visitors.

IV.8.7.6. Noctuidae (unidentified)

Forty observations on uncollected specimens were made. Between 9.VII and 16.VII, 10 were observed on *Dryas integrifolia* of which 5 were observed probing for nectar; 2 (10.VII) were noted with their tarsi gripping the petals of their flowers, while their abdomens hung over the rim of the corollas and their heads were held over the nectaries into which their tongues were inserted. One (16.VII) was watched as it approached a flower; it landed on the ground in front of it, then crawled up onto the corolla to feed. Between 13.VII and 20.VII at Gilman Camp 17 were observed on *Arnica alpina*, 3 of which were noted actively probing into the disc florets. One (18.VII) was watched as it approached an inflorescence; it landed on the back and crawled over onto the front and began to feed (cf. *Anarta (Hadena) richardsoni*; *Lasiestra leucozycla*). On 13.VII, at Gilman Camp, I was 1 taking nectar from *Potentilla* sp. (prob. *nivea*). On 19.VII at Hazen Camp 12 specimens were seen probing into the flowers of *Polygonum viviparum*.

Unidentified noctuid larvae were recorded feeding on the inflorescences of staminate *Salix arctica* (1,10.VI.1967) and *Saxifraga oppositifolia* (1,2.VI; 2,8.VI; 13,1.VI.1967).

IV.8.8. Pyralidae

One species of Pyralidae, *Udea torvalis* Möschl. has been collected from Ellesmere Island (Downes, 1966). It has not been recorded in



association with flowers, although it is likely to be a flower visitor.

#### IV.9.1. Lycaenidae

Two species are known from the high arctic of Canada; *Lycaena feildeni* McLach. and *Plebius aquilo* Bdv. The Lycaenidae are well known flower visitors.

##### IV.9.1.1. *Lycaena feildeni* McLach.

This species is the least common butterfly around Hazen Camp. Only 4 observations of this species on flowers were made. On 16.VII, 1 male with its wings held open\* was watched as it walked over the spike of *Polygonum viviparum*. On 22.VII 1 female (probably) was collected as it imbibed nectar from *Taraxacum* sp. (prob. *arctogenum*). Neither of these specimens carried pollen. One other was recorded on *Taraxacum* sp. (prob. *arctogenum*) presumably during this period. On 17.VII at Gilman Camp, 1 individual with its wings held open was observed imbibing nectar from *Arnica alpina* but it escaped.

##### IV.9.1.2. *Plebius aquilo* Bdv.

Twenty records of this species visiting flowers were made in 1967. Most of the specimens were not captured. At Gilman Camp 4 were observed on *Arnica alpina* (1,14.VII; 1,17.VII; 2,19.VII); 2 of these were observed actively imbibing nectar, their proboscides in the disc florets; 3 were noted with their wings held open\*; 1 female was collected and was clean of pollen. At Hazen Camp, 1 was observed imbibing nectar

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\* The position in which the wings are held has thermoregulatory significance (Kevan and Shorthouse, 1970).



from *Potentilla nivea* (16.VII) and 2 others seen resting on a pistillate catkin of *Salix arctica* (19.VII) with developing seed pods. Between 17.VII and 26.VII, 13 were observed on *Polygonum viviparum*. One male was collected on 17.VII after it had imbibed nectar from several flowers, it held onto the spike vertically with its head lowermost and its wings held open; I could not find pollen on it. On 19.VII, 11 specimens were observed exactly as above, one was watched on one spike for 2 minutes. On 26.VII, 1 male was collected in exactly the same circumstances as above, it carried no pollen. All the above specimens were observed on the insolated sides of the spikes upon which they were feeding.

Hocking (1968) observed 1 specimen imbibing nectar from a female *S. arctica* catkin and 3 specimens, 1 of which was imbibing nectar, on *Dryas integrifolia*.

#### IV.9.1.3. Lycaenidae (larvae)

Five unidentified larvae were collected as they ate the flowers of *Saxifraga oppositifolia* (3,1.VI; 2,9.VI.1967).

#### IV.9.2. Nymphalidae

Nymphalids are well known visitors to flowers, as is also true in tundra areas (Chernov, 1966). There are two species at Hazen Camp, *Boloria polaris* Bdv., and *Boloria chariclea* Schneid. (Oliver, 1963; Downes, 1966).

##### IV.9.2.1. *Boloria polaris* Bdv.

Five specimens of this species were collected from flowers in 1967. On 20.VI, 1 was collected as it imbibed nectar from *Saxifraga oppositifolia* and 1 was collected on *Dryas integrifolia* in the same circumstances. The latter specimen was followed as it visited 2





flowers. On 28.VI, 1 female was collected as it imbibed nectar while hanging onto the edge of the corolla of *D. integrifolia*, its proboscis extended over the stamens and into the nectaries. It carried pollen on its head and tongue. On 9.VII, behind Mt. McGill at an altitude of about 600 m, 2 males were collected as they fed on the nectar of *D. integrifolia*, both were well dusted with pollen on their heads, eyes, and palpi.

Chernov (1966) mentions this species as a flower visitor in the Soviet arctic.

IV.9.2.2. *Boloria* sp. (prob. *polaris*)\*

On 1.VI.1967, 1 specimen was seen imbibing nectar from *Saxifraga oppositifolia*. On 3.VI and 14.VI, single individuals were seen imbibing nectar from staminate catkins of *Salix arctica*. On 20.VI and 26.VI, single individuals were observed as they imbibed nectar from *D. integrifolia*.

IV.9.2.3. *Boloria chariclea* Schneid.

This species emerges later than *B. polaris* and is generally more abundant (Downes, pers. comm.). Nine specimens were collected from flowers in 1967. On 17.VII, 1 male carrying pollen on its head and tongue was taken as it imbibed nectar from *Dryas integrifolia*. On 19.VII, 1 male was collected as it imbibed nectar from *Polygonum viviparum*. On 22.VII, 1 female was collected as it imbibed nectar from *Stellaria longipes*. At Gilman Camp, between 14.VII and 21.VII, 3 males (14.VII, 17.VII, and 18.VII), 2 females (20.VII and 21.VII)

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\* Five specimens collected before the first confirmed collection of *B. chariclea* are included here.



and 1 unsexed (16.VII) were collected from *Arnica alpina*. Two of the males were observed feeding on nectar, and 1 was resting; the 2 females were both resting. All carried pollen, particularly on their proboscides, tarsi, and palpi.

Chernov (1966) mentions this species as a flower visitor in the Soviet arctic.

IV.9.2.4. *Boloria* sp. (prob. *chariclea*)\*

Eight specimens were observed on *D. integrifolia* flowers; all were observed with their proboscides into the nectaries imbibing nectar (2, 1.VII; 2, 16.VII (1 from Gilman Camp); 4, 17.VII.1967). Twenty-four specimens were observed on *Arnica alpina*, all at Gilman Camp: only one was observed resting with its wings closed and its tongue coiled (16.VII); the others were imbibing nectar (13 observations) or their activity was not determined (10 observations). Six of the 13 were watched as they walked around the disc inserting their proboscides into numerous florets. One individual was watched as it flew from feeding at one bloom to commence feeding at a second. On 19.VII, one specimen was seen on a pistillate catkin of *Salix arctica*, and another imbibing nectar from *Taraxacum* sp. (prob. *arctogenum*). On 16.VII and on 26.VII single individuals were seen imbibing nectar from *Polygonum viviparum*; one (16.VII) walked over the insolated side of the spike, thrusting its proboscis into the flowers as it went, it then rested for 1.5 minutes at the apex of the spike before flying off.

In 1968 I recorded butterflies feeding on the nectar of *Pedicularis*

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\* Thirty-six specimens collected after the last confirmed collection of *B. polaris* are included here.



*arctica*. P. S. Corbet made a similar observation of a male in 1966. I watched one as it fumbled its proboscis up the mid convolution of the labellum and inserted it into the corolla tube.

Hocking (1968) recorded *Boloria* sp. from the inflorescences of *Salix arctica* (staminate), *Dryas integrifolia*, *Potentilla* sp., *Epilobium latifolium* at Hazen Camp, and Chernov (1966) considers the flowers visited by *Boloria* spp. in the Soviet arctic.

One larva was found feeding on a flower of *D. integrifolia* on 10.VII.1967.

#### IV.9.3. Pieridae

The Pieridae are well known flower visitors (cf. Müller, 1873: 467) as is also true in arctic areas (Chernov, 1966). At Hazen Camp there is one species, *Colias hecla* Lef. (Oliver, 1963; Downes, 1966).

##### IV.9.3.1. *Colias hecla* Lef.

Thirteen of these insects were observed in flowers in 1967. On 8.VII, 1 specimen was observed imbibing nectar from a flower of *Dryas integrifolia*. On 19.VII.1966, Dr. P.S. Corbet saw one male and one female on flowers of *D. integrifolia*. On 16.VII, 1 specimen was observed to settle on a flower of *Papaver radicatum* where it rested for 8 seconds before flying off. On 19.VII, 1 male was collected as it imbibed nectar from a *Taraxacum* (prob. *arctogenum*) inflorescence. It carried no pollen. The remaining 10 specimens were observed on *Arnica alpina* at Gilman Camp between 14.VII and 21.VII; 2 males were collected (14.VII & 21.VII) neither carried pollen; 1 individual (14.VII) was watched as it visited 3 inflorescences even attempting to find nectar in the back of one; 5 others were observed imbibing nectar from the





disc florets (2,14.VII; 3,17.VII); and single individuals with undetermined activity on two other occasions (16.VII, 19.VII).

Hocking (1968) recorded 1 specimen on flowers of each of *D. integrifolia* and *Taraxacum* sp. On Melville Island Mosquin and Martin (1967) recorded 11 specimens of this species on *Astragalus alpinus*. Chernov (1966) mentions this species as a flower visitor in the Soviet arctic.

#### IV.9.2. *Colias* Spp.

Several species of *Colias* are noted by Chernov (1966) as flower visitors, including *Colias nastes* Bdv. which was also recorded once on *Astragalus alpinus* on Melville Island by Mosquin and Martin (1967).

#### IV.10. *Tipulidae*

Tipulidae are noted as flower visitors by Müller (1873), and Chernov (1966) reports that they are sometimes found in large numbers on flowers in the arctic, listing 3 species of *Tipula* and 2 of *Prionocera* associated with *Caltha palustris* and *Dryas punctata* at Anabarski Inlet.

Of the 5 species occurring at Hazen Camp only one, *Tipula arctica* Curtis was encountered on flowers. On 14.VI.1967 a single specimen was observed on a staminate catkin of *Salix arctica*, it was well dusted with pollen, but its activity was not ascertained. In July 1966 a single specimen was observed with its mouthparts in the nectar of a flower of *Saxifraga tricuspidata*. *Tipula arctica* is a clumsy flier, and stays close to the ground. Thus, on several occasions they were noted bumping into the inflorescences of *Dryas integrifolia*, *Salix arctica*, and others. Hocking (1968) records a single observation of undetermined activity of this species on a *D. integrifolia* blossom.



IV. 11. Chironomidae

Although Oliver (1963) lists 54 species of Chironomidae from Hazen Camp, he (1968) remarks that only the adults of 2 species, *Smittia extrema* Holmgren (= *velutina* Lundbeck) and *S. polaris* Kieff. n. comb. have been observed imbibing nectar. Hocking (1968) records only one instance of many undetermined Chironomidae imbibing nectar from *Saxifraga oppositifolia* from more than 59 different combinations of chironomids on flowers.

IV.11.1. Tanypodinae, Procladius sp.\*

One female was collected from a flower of *Dryas integrifolia* on 27.VI.1967.

IV.11.2. Orthocladiinae

IV.11.2.1. Protanypus caudatus Edw.

Two males (15.VII, 21.VII) collected from *Arnica alpina* at Gilman Camp. One was resting on a ray floret, the other, dusted with pollen, was on the disc. On 17.VII a female was found resting on a *Draba* sp. flower.

IV.11.2.2. Cricotopus spp.

One female was found on *Dryas integrifolia* (27.VI) at Hazen Camp and 2 resting on *Arnica alpina* (15.VII, 18.VII) at Gilman Camp. The first mentioned specimen carried no pollen, had ingested none, and had follicles at stage 3.

IV.11.2.3. Heterotrissocladius subpilosus (Kieff.)

I collected 5 females and 1 male at Gilman Camp. The male (16.VII)

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\* *Procladius* sp. No. 2 of D. R. Oliver.



was taken on *Lesquerella arctica*. The females (2,18.VII; 3,21.VII) were taken on *Arnica alpina*; 4 carried pollen, none had ingested any. Those collected on 21.VII had spent ovaries.

IV.11.2.4. *Psectrocladius* sp.

On 13.VII I found 1 female on the petals of a *Dryas integrifolia* flower.

IV.11.2.5. *Trissocladius* sp.

On 3.VII one male was taken on *Papaver radicatum*. On 13.VII one female was found deep in the corolla tube of *Pedicularis arctica*.

IV.11.2.6. *Limmophyes* sp. or spp.

Oliver (1963) records 5 species of *Limmophyes* from Hazen Camp, of which at least 3 have been collected on flowers (Hocking, 1968).

I collected 19 females and 2 males from *Saxifraga oppositifolia* on 15.VI.1967. Only 3 females were dusted with pollen. On the same day I found 18 females noted as imbibing nectar, and 9 males on staminate catkins of *Salix arctica*. One female (16.VI) had ovarian follicles at stage 4. All were dusted with pollen. I also collected 18 females, noted as imbibing nectar, and 1 male on pistillate catkins. On 27.VI, 6 females were found deep in the corolla tubes of *Pedicularis arctica*. They were oriented head down near the nectaries. On 29.VI a further 21 females were found in exactly the same positions. I found their ovarian follicles at stage 2 in 8 specimens, stage 3 in 1, stage 4 in 2, unknown in 5, and spent in 4. I found 4 males with the females on 29.VI. On 13.VII I collected 1 other female with spent ovaries from a flower of *P. arctica*. I took 3 females from *Dryas integrifolia* (1,8.VII; 1,9.VII; 1,13.VII); the first two were dusted with pollen,





and all 3 were apparently inactive. The first specimen had stage 3 follicles, the other had spent their ovaries. On 3.VII I took 3 females from *Papaver radicatum*; on 9.VII 1 male, dusted with pollen, on *Ranunculus sulphureus*; and on 8.VII 1 male, without pollen, on *Erigeron eriocephalus*.

IV.11.2.7. *Metriocnemius ursinus*

A few specimens were collected in association with *Saxifraga oppositifolia* between 21.VI and 25.VI.1966.

IV.11.2.8. *Smittia velutina* Lundbeck (= *extrema* Holmgren)

I collected 479 females from *Saxifraga oppositifolia* flowers between 31.V and 23.VII.1967 (1, 31.V; 41, 1.VI; 4, 2.VI; 57, 3.VI; 95, 7.VI; 43, 8.VI; 41, 9.VI; 64, 10.VI; 36, 11.VI; 50, 12.VI; 26, 15.VI; 20, 9.VII; 1, 23.VII.1967). Of 257 examined for external pollen dusting, 138 (53.7%) carried pollen grains. All were found deep in the corollas, apparently imbibing nectar as their mouthparts were applied to the droplets of nectar at the bases of the filaments and around the bases of the ovaries. I dissected the guts of some and found most of them distended (cf. McAlpine, 1965) with clear syrupy nectar. Of 272 dissected, none had ingested pollen. I collected 193 females from staminate catkins of *Salix arctica* (7, 3.VI; 5, 7.VI; 20, 9.VI; 155 (from 3 catkins), 12.VI; 1, 15.VI; 5, 16.VI.1967). All were dusted with pollen, and all were taken from deep within the pubescence of the catkins wherein they had their mouthparts applied to the nectar. Only the posterior ends of their abdomens were visible. None of the 58 dissected had ingested pollen. I found only 1 female (15.VI) on pistillate catkins, but I attach no significance to this



as it probably reflects poor collecting. In 1966 and 1968 many chironomids, including *S. velutina* were found on pistillate catkins as Hocking (1968) and McAlpine (1965) also report. Five females were found in the flowers of *Dryas integrifolia* (1, 9.VI; 3, 8.VII; 1, 15.VII). One held itself head down between the anthers and pistils, and was imbibing nectar. Only 1 (of 4 examined) was dusted with pollen; none had ingested any. I found 3 females deep in the corolla tubes of *Pedicularis arctica* (1, 27.VI; 2, 29.VI). They were directed head down and presumed imbibing nectar. None carried pollen or had ingested any. On 21.VII one female was found on *Potentilla nivea* in the same position as described for that on *D. integrifolia* (15.VII). Hocking (1968) also records females of this species from the flowers of 6 other species of plant, and males from staminate *Salix arctica*. I did not record any males of this species on flowers, but these records may be included under *Smittia* spp.

I dissected 337 females to examine the development of their ovarian follicles (see Table 2).

The almost constant proportion (65%) of the population with ovarian follicles at stage 3, particularly at the beginning of their season when large numbers were caught, has several implications about their life history. Oliver (1968) found that 9 species of chironomid emerge with almost mature (stage 3) or mature follicles, and that maturation takes 3 days or less. Although these observations were not made on *Smittia* spp. I think that a similar time duration could well be postulated for follicular maturation from stage 3 in *Smittia velutina* as well as other species of chironomid. Thus it seems that the population of *S. velutina* on flowers is constantly changing as



Table 2.

Seasonal distribution of stages of ovarian follicle development of *S. velutina* on flowers in 1967 at Hazen Camp.

<u>Date</u>	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>Spent</u>	<u>Unknown</u>	<u>% stage</u>	<u>3</u>	<u>Flower</u>
31.V	0	0	1	0	0		--		<i>S. oppositifolia</i>
1.VI	1	1	12	2	0		75		<i>S. oppositifolia</i>
2.VI	0	0	4	0	0		--		<i>S. oppositifolia</i>
3.VI	0	1	21	0	0		95		<i>S. oppositifolia</i>
3.VI	0	0	5	2	0		--		<i>S. arctica</i>
7.VI	0	4	21	6	0		68		<i>S. oppositifolia</i>
7.VI	0	2	2	0	0		--		<i>S. arctica</i>
8.VI	0	2	15	4	0		71		<i>S. oppositifolia</i>
9.VI	2	4	21	6	0	1	64		<i>S. oppositifolia</i>
9.VI	0	0	17	1	0	4	94		<i>S. arctica</i>
10.VI	2	10	29	7	0		60		<i>S. oppositifolia</i>
11.VI	1	5	23	5	0		68		<i>S. oppositifolia</i>
12.VI	3	3	15	3	2		58		<i>S. oppositifolia</i>
12.VI	0	0	20	0	0		100		<i>S. arctica</i>
15.VI	0	0	4	10	4		22		<i>S. oppositifolia</i>
16.VI	1	0	1	3	0		--		<i>S. arctica</i>
27.VI	0	0	0	1	0		--		<i>P. arctica</i>
29.VI	0	0	1	0	1		--		<i>P. arctica</i>
8.VII	0	0	0	0	3		--		<i>D. integrifolia</i>
9.VII	0	2	7	4	3		43		<i>S. oppositifolia</i>
15.VII	0	0	1	0	0		--		<i>D. integrifolia</i>
23.VII	0	0	0	0	1		--		<i>S. oppositifolia</i>
Total	10 3%	34 10%	220 65%	54 16%	14 4%	5 2%			





is implied by the diel changes of distribution of chironomids on clumps of flowers of *Saxifraga oppositifolia* with geographical aspect, but the constancy of diel distribution with solar aspect (Table 31). The preponderance of stage 3 individuals may reflect the fact that the follicles are well developed at eclosion, or that 3 is a long stage, or both. The later stage 1 and stage 2 observations can be interpreted as parts of the further ovarian cycles.

Nectar is probably required as fuel for flight for mating and hunting oviposition sites.

#### IV.11.2.9. *Smittia* spp.

Oliver (1963) lists 2 other species of *Smittia*, *S. polaris* Kieff. n. comb. and *S. polymorpha* Ander. Both of which have been recorded on flowers by Hocking (1968) and *S. polaris* by McAlpine (1965).

I collected 4 males of *Smittia* sp. or spp. from the flowers of *Saxifraga oppositifolia* (1, 2.VI; 1, 3.VI; and 2, 7.VI.1967). These may have been *S. velutina*. They were resting on the petals, anthers, and stigmas; all but 1 carried pollen. Seven male and one female *Smittia* sp. or spp. were taken from staminate catkins of *Salix arctica* (including the female) were examined and found carrying pollen.

I collected 1 female deep in the corolla tube of a flower of *Pedicularis arctica* (29.VI). Another (12.VII) with spent ovaries, and without pollen externally or internally, and 1 at Gilman Camp (18.VII) were collected from *Potentilla* sp. (probably *nivea*) flowers.

Three males (2, 1.VII; 1, 12.VII) were found on *Dryas integrifolia* flowers, 2 were dusted with pollen. Eight females (2, 27.VII; 4, 8.VII; 1, 12.VII; 1, 17.VII) were found on *D. integrifolia*, 6 were dusted with pollen. Ovarian follicular stages ranged from 3 (27.VI) to 4



(8.VII) to spent ovaries (8.VII; 17.VII). Females were found on pistillate catkins of *Salix arctica* (1, 7.VI), resting on flowers of *Papaver radicum* (1, 19.VII) and *Lesquerella arctica* (2, 3.VII). Neither of the last two were dusted with pollen, one had ovarian follicles at stage 3, the other was spent.

IV.11.2.10. *Corynoneura* sp. *scutellata* Winnertz

On 13.VII I collected 2 females from deep in the corolla tubes of *Pedicularis arctica* flowers where they were assumed to be imbibing nectar; 1 carried pollen. On the same day 2 other females were found right down at the bases of filaments and styles, presumably imbibing the nectar, they were dusted with pollen. At Gilman Camp on 20.VII I found 8 females and 4 males on *Stellaria longipes* flowers all with their heads down into the nectar as they stood on the sepals and petals. The follicles of 2 (13.VII) were late in stage 3 and at stage 4. None had ingested pollen.

IV.11.2.11. Orthocladiinae, genus unknown (previously designated *Prosmittia nansenii* Kieff. n. comb. (Oliver, 1963; pers. comm.)).

I collected 1 male from *Potentilla* sp. (prob. *nivea*) (15.VII) and 1 female from *Dryas integrifolia* (3.VII). Neither carried pollen. Hocking (1968) records 1 male on *D. integrifolia* and 2 "flying over" *Saxifraga oppositifolia*. Between 21.VI and 25.VI.1966 I collected a few specimens from *Saxifraga oppositifolia*.

IV.11.2.12. *Paraphaenocladus despectus* (Kieff.)

I collected 15 females (1, 11.VI; 12, 12.VI; 1, 15.VI; 1, 9.VII. 1967) from *Saxifraga oppositifolia*. They were found deep in the



corollas in the same position as *Smittia velutina* and presumed to be imbibing nectar. Eight carried pollen grains, none had ingested pollen. Five males were collected on these flowers (1, 11.VI; 4, 12.VI) none carried pollen nor had ingested any. These too were deep in the corolla and possibly imbibing nectar. Five females were found on pistillate inflorescences of *Salix arctica*, their heads were directed inwards and their mouthparts applied to the nectar. One female was found deep in the corolla tube of *Pedicularis arctica* on 27.VI presumably imbibing nectar. Examination of the follicles revealed stage 3 predominated (10 observations 11.VI and 12.VI) with 2 observations at stage 2 (12.VI; 27.VI).

I propose that the explanation of ovarian maturation for *Smittia velutina* is applicable here.

#### IV.11.2.13. Orthoclaadiinae (unidentified)

I collected 2 females on *Dryas integrifolia* (28.VI; 13.VII), the latter found at the base of the filaments, perhaps imbibing nectar. Only the former carried pollen, and then only 1 grain. The male was also collected from *D. integrifolia* at Gilman Camp (13.VII) as prey of a male of *Rhamphomyia filicauda*.

#### IV.11.3. Chironominae, *Microspectra* Sp.

On 4.VII 1 male *M. groenlandica* was found on *Dryas integrifolia*, it carried no pollen and had ingested none. On 15.VII, at Gilman Camp, 1 female *Microspectra* sp. was observed walking around the petals of a *Potentilla* sp. (prob. *nivea*) flower, waving its antennae. It was lightly dusted with pollen, but had ingested none.





#### IV.12. Ceratopogonidae

The number of Ceratopogonidae species from Hazen Camp is not known; Oliver (1963) lists *Forcipomyia* sp., *Ceratopogon* 4 spp., and *Culicoides* sp. as determined by J. A. Downes; however Downes (pers. comm.) remarked that he is not sure if there are really 2 species of *Ceratopogon* (*Isohelea*) at Hazen Camp. Some species of Ceratopogonidae are noted nectar feeders (Downes, 1958). Downes (1955) recorded a pollen eating species, *Atrichopogon pollinivorous* Downes, feeding on individual pollen grains of honey-suckle.

##### IV.12.1. *Forcipomyia* (*Thyridomyia*) Sp.

*Forcipomyia* spp. are frequently blood suckers of other insects (Imms, 1964: 261). On 13.VII one female with its head well down between the stamens and pistils into the nectar was collected from a flower of *Dryas integrifolia*.

##### IV.12.2. *Ceratopogon* (*Ceratopogon*) Sp.

On 8.VII.1967 one female was collected from a flower of *D. integrifolia*. Its activity was unknown.

##### IV.12.3. *Ceratopogon* (*Isohelea*) Sp. or Spp.

Three specimens of this genus were collected in flowers. On 8.VII, 1 male and 1 female were collected from *D. integrifolia*; and on 13.VII, 1 female was collected from deep within the corolla tube of a *Pedicularis arctica* flower. Their activities were not ascertained, but from their positions in the flowers they were presumably imbibing nectar. Downes (pers. comm.) has collected this genus from various flowers.



IV.12.4. *Culicoides* Sp.

*Culicoides* sp. are bloodsuckers on vertebrates. Two males (27.VI; 8.VII) and 1 female (8.VII) were collected on flowers of *D. integrifolia*. On 18.VII, at Gilman Camp, 1 female was collected from an inflorescence of *Arnica alpina*.

IV.13. *Culicidae*

Knab (1907) considered mosquitoes as flower visitors. Hocking's (1953) review lists 21 species of Culicidae associated with many species of flowers, although Müller (1873) lists only *Culex pipiens* (Knab). The majority of Hocking's references are to *Aedes* spp. (12+), *Anopheles* accounts for 2 species, *Culex* for 4 species, *Culiseta* for 2 species, and 1 species each of *Mansonia* and *Megarhinus*. In the arctic *Aedes* spp. have been reported feeding on the nectar of flowers by Longstaff (1923), Fridolin (1936), Hocking and Twinn (1950), West and Jenkins (1951), Hocking (1953, 1968), Knight and Jachowski (1956), Corbet (1964), Chernov (1966), and basking on flowers (Hocking and Sharplin, 1965).

IV.13.1. *Aedes (Ochlerotatus) impiger* Walker

Only 2 specimens of undetermined activity were collected, both from *Dryas integrifolia* flowers. One male was collected on 26.VI, and 1 female on 28.VI, both carried pollen grains on their hairy bodies, but neither had ingested any, no solid material was visible in their guts. The ovaries of the female were at stage 2. Hocking (1968) records this species from male *Salix arctica* (1 male), *Stellaria* (1 female), *Potentilla* (1 female), and *Dryas integrifolia* (3 females, 1 male). Only one of the females taken on *D. integrifolia* was observed



feeding on nectar, all the others are noted as basking or resting.

IV.13.2. *A. (O.) nigripes* Zetterstedt

Twenty specimens were collected from flowers in 1967. Of the 8 females, caught between 4.VII and 16.VII, all were on *D. integrifolia*; 4 were actively feeding on nectar and of these 1 had its gut distended with blood (see Corbet and Downe, 1966); 1 was the prey of *Rhamphomyia filicauda* (male) (13.VII); and the remaining two were basking or resting; one of them was watched for over five minutes, during which time it remained almost stationary. Seven were carrying pollen externally, but none showed evidence of having eaten any. Ovarian follicles were at all stages of development; 1 at stage 1, 1 at stage 2, 2 at stage 3, and 2 at stage 4; they were not examined to determine whether they had laid eggs.

The 12 males were collected between 25.VI and 17.VII, 7 as they were feeding on nectar of *D. integrifolia*, and 3 apparently basking in these flowers. Two were collected from *Arnica alpina* at Gilman Camp, but their activity was not determined.

Hocking (1968) records 1 female from each of male *Salix arctica* and *Stellaria*, one male from each of *Potentilla nivea* and *Arnica alpina* and one male and 2 females from *D. integrifolia*, one of which was feeding on nectar. The activities of the remainder are noted as basking, resting, or uncertain.

When these animals feed on nectar from *D. integrifolia* they do not need to duck their heads as far as do empidids and muscids as they have longer mouthparts. Nevertheless, on 6 occasions they were observed feeding, their proboscides between the stamens and pistils





so that their heads and nota touched the anthers, and on 2 occasions they had their proboscides pushed down through the filaments, so that their heads and nota and pleura were in contact with the anthers. Generally, they assume a vertical position on the flowers, with their heads uppermost (6 observations) or with their heads down (3 observations).

#### IV.13.3. *Aedes* Spp.

Twenty-three observations were made on mosquitoes which eluded capture on flowers. Males were wary and took flight on my approach, females became interested in feeding from me, and mingled with the mosquitoes at my head, no doubt alerted by the noise of these.

Thirteen males were seen on *D. integrifolia* between 27.VI and 15.VII; 7 were feeding on nectar, 2 with their nota and heads touching the stigmas, I did not observe the postures of the other 5. One male was seen on *A. alpina* at Gilman Camp (18.VII). Seven females were seen on *D. integrifolia* between 27.VI and 15.VII, 3 were feeding on nectar. On 28.VI, 1 was seen attempting to probe into the corolla tube of *Pedicularis arctica*. It attempted to run its proboscis down the mid-convolution in the labellum of the flower three times. Although it inserted its mouthparts into the tube it was unable to obtain nectar as the tube was too long, it then flew off. I watched approaches of 1 male and 1 female to a *D. integrifolia* flower on 13.VII. The female flew directly up to the flower and landed without hesitation. The male, on the other hand, made three slow passes at the flower, then landed on the back side where it rested for 2.5 minutes before crawling over onto the front of the flower where it began to feed on nectar. Three observations on the orientation of mosquitoes on flowers showed



all oriented vertically, with their heads uppermost.

Hocking (1968) lists 12 unidentified *Aedes*; 1 male and 1 female taking nectar from *Salix arctica*, 4 males and 3 females basking on *D. integrifolia*, 2 females basking on *Potentilla* sp. (probably *nivea*), and 1 female on *Epilobium latifolium*, but none on *Papaver radicum* (cf. Hocking and Sharplin, 1965).

#### IV.14. Sciaridae

Sciaridae are not noted anthophiles, however Müller (1873) recorded *Sciara thomae* L., from Umbelliferae and Compositae. Holmgren (1869) found *S. atrata* Say on *Cerastium alpinum*. At Hazen Camp 7 species of *Bradysia* have been recorded (Oliver, 1963), but this genus is not well known taxonomically and it is impossible to assign specific names to the specimens I collected.

Twenty-seven specimens representing at least 6 species were collected between 21.VI and 20.VII from flowers of 7 species of plants. On 21.VI, 2 females were collected as they were seen imbibing nectar from flowers of *Saxifraga oppositifolia*. Between 19.VI and 24.VII, 2 males (26.VI and 8.VII); 9 females (19.VI to 16.VII), and 2 unsexed (24.VII) were taken from flowers of *Dryas integrifolia*, 1 female was feeding on nectar, its notum against the stigmas, another was running over the anthers. One male (29.VI) and 5 females (29.VI to 12.VII) were found deep in the corolla tubes of *Pedicularis arctica*, where I assume they were feeding on nectar. Six females were taken on flowers of *Lesquerella arctica*, all feeding on nectar; 2 with their dorsa against the pistils. Two females were taken as they fed on the nectar of *Potentilla* sp. flowers at Gilman Camp (15.VII and 18.VII).



Two females, one with its abdomen sticking out of a disc floret into which its head was deeply inserted, were found in inflorescences of *Arnica alpina* (18.VII and 20.VII). One was removed from a flower of *Stellaria longipes*. Eleven specimens had pollen on their bodies, usually only very few grains on the thorax or head, and on one occasion between the pro-coxae. These insects are not very hairy so it is unlikely that they could become well dusted with pollen.

McAlpine (1965) noted a single female on *D. integrifolia*. It was imbibing nectar with its head forced down between the stamens, there it "lapped at each nectary within reach of its short, fleshy mouthparts." Hocking (1968) noted several on both male and female catkins of *S. arctica*. In 1968, I collected specimens from *Draba Bellii* as they ran in and out of the flowers to feed on nectar.

The gut contents of all specimens were examined. I found only clear liquid, assumed to be nectar. Ovarian follicles were noted at stage 2 in 8 females (21.VI to 20.VII), at stage 3 in 10 females (27.VI to 18.VII), and at stage 4 in 4 females (21.VI to 8.VII). It seems that these flies visit flowers at most stages of their adult lives, but tend to feed on nectar more when the ovarioles are at stages 2 and 3. Ovarian follicular stage 1 may be passed in the pupal stage, as in some species of Chironomidae (Oliver, 1968). Flower visiting by females with ovarioles at stages 2 and 3 may be linked with fuel for mating flights, or searching for oviposition sites.

#### IV.15. Cecidomyiidae

Oliver (1963) lists two species of cecidomyid from two sub-families, Lestermiinae and Cecidomyiinae. Cecidomyiidae are not well known





flower visitors. None were collected from flowers at Lake Hazen in 1967. Hocking (1968) recorded 2 from male *Salix arctica* catkins and Downes (1964) mentions that there is a cecidomyid larva "of unknown food-habit that lives on the catkins." It is possible that Hocking's records are of ovipositing females, or at least females searching out suitable oviposition sites. Pistillate catkins would be more suitable, on which I have occasionally found small sculptured white eggs, perhaps belonging to these insects.

#### IV.16. Dolichopodidae

Of the 2 species occurring at Hazen Camp (Oliver, 1963), only one, *Dolichopus dasyops* was collected on flowers. Two males were collected from the flowers of *Stellaria longipes* (s. lat.) at Gilman Camp on 20.VII, and 1 male from the flowers of *Polygonum viviparum* at Hazen Camp on 19.VII.1967 where it was feeding on nectar. Hocking (1968) records one female from the flowers of *Stellaria* sp.

Müller (1873) reports that *Dolichopus aeneus* Deg. L. was taken from the inflorescence of *Sium latifolium* (Umbelliferae) and indexes a reference to *Gymnopterus chaerophylli* Mgn., L., also on an umbellifer. Malloch (in Imms, 1964) reports that many species occur on flowers, undoubtedly feeding on nectar. *Hercostomus* is reported to feed on pollen by Laurence (1953), but there is no evidence to suggest that *D. dasyops* does; dissections revealed no solid material in their guts. No pollen was found externally on these shiny insects.

#### IV.17. Empididae

At Hazen Camp there are 4 species of Empididae; *Rhamphomyia*



*filicauda* Lundbeck, *R. hoeli* Frey, *R. (Dasyrhampomyia) nigrita* Zetterstedt, and *R. ursinella* Melander. The genus *Rhampomyia* belongs to the subfamily Empidinae, the members of which exhibit specialized sexual differentiation in hunting and feeding habits as adults (Downes, in press). Empididae are generally known to visit flowers for nectar (Downes and Smith, 1969; Tuomikoski, 1952; Müller, 1873; Knuth, 1906-1909) and *Anthalia bulbosa* Melander (Ocydromiinae) may feed on pollen (Downes and Smith, 1969). Porsch (1966) also mentions *Empis pennipes* L. and *E. ciliatopennata* Strobl. as pollen feeders on *Veronica* sp., but this record is dubious (cf. Downes and Smith, 1969).

#### IV.17.1. *Rhampomyia filicauda* Lundbeck

Between 16.VI and 31.VII.1967, 231 specimens of this abundant empidid were collected or observed or both, mainly from the flowers of *Dryas integrifolia* (214 records). I recorded 145 females on these flowers from 19.VI until 31.VII, while males were found 57 times from 16.VI until 31.VII. Between 5.VII and 16.VII, 20 records were made of insects which were not collected. Twelve individuals were seen as they imbibed nectar, only one was seen as it commenced to feed. The process was identical to that of *R. nigrita*. The fly approached one flower hesitantly, hovering momentarily, passing it by, then repeating this procedure in front of another flower, upon which it landed. It then probed down with its fore tarsi, presumably to taste for nectar (vide Dethier, 1963: Ch. V), upended itself and started to imbibe nectar from the nectaries around the flower. McAlpine (1965) records abdominal pumping motions accompanying feeding. They feed in the same three positions described for *R. nigrita*, but 6 were noted



with their nota touching the stigmas, while only 1 was seen the other way, with its notum touching the anthers; 2 were seen as they imbibed nectar through the filaments from the side. Most of the specimens were observed as motionless on the flowers, sometimes remaining so for several hours (cf. *R. nigrita*). They may take advantage of the ameliorated micro-climate within the flowers after having fed on nectar. In contrast to *R. nigrita*, these flies are more catholic in the way in which they rest or bask on flowers. During sunny weather 48 were observed basking, 13 oriented horizontally to the right, and 7 horizontally to the left; 4 were vertical with their heads down and 3 vertical, heads uppermost; 2 each were oriented between head uppermost and horizontally left and right.

Females were also collected from other flowers; 1 (3.VII) *Lesquerella arctica*, 1 (10.VII) *Papaver radicatum*, 3 (15.VII-18.VII, Gilman) *Arnica alpina*, 2 (18.VII-19.VII) *Potentilla* sp. (probably *nivea*), 3 (19.VII-21.VII) *Polygonum viviparum*. Males were also collected on *Papaver radicatum* (3, 1.VII-13.VII) and *A. alpina* (2, 18.VII-21.VII, Gilman Camp). Unsexed flies were observed on *Potentilla* sp. (probably *nivea*) (1, 15.VII) and *A. alpina* (1, 17.VII, Gilman Camp). McAlpine (1965) noted many males and females on *D. integrifolia*, but states that he did not see this fly on any other flowers at that time; however he mentions a long series of them collected from Coral Harbour, Southampton Island, N.W.T. by G. E. Shewell which were also taken on *D. integrifolia* flowers, but that also one male and 1 female were taken on *Salix* sp. (probably *arctica*) then. Hocking (1968) records 10 males and 16 females resting on *D. integrifolia* and 1 male on *Potentilla* sp.





The only other activity noted for this species on flowers, apart from feeding on nectar, basking, and resting was on 13.VII.1967 when 2 males were collected on *D. integrifolia* with prey, presumably for their courtship behaviour (see Downes, in press). One was collected at Hazen Camp and had a female of *Aedes nigripes*, while the other was collected at Gilman Camp with a small chironomid too mutilated for identification.

Of 210 flies examined for superficial pollen, only 21 were without it. Over 200 dissections failed to show that these flies ingested pollen grains.

The ovarian follicles were examined in 154 females; 27 had ovarioles at stage 1, 59 at stage 2, 48 at stage 3, 18 at stage 4, and 2 (at the end of the summer) had no follicles and were assumed spent). Flies with stage 1 follicles appeared on 19.VI and lasted until 26.VI, occurring again with 9 flies on 9.VII, after which 2 others were found (13.VII and 25.VII). Flies with stage 4 follicles were first taken on 28.VI and subsequently throughout the season, with peaks on 4.VII and 12.VII. The data are sporadic according to the availability of anthophilous individuals, and the effects of previous weather. The data show that these insects tend to imbibe nectar when their follicles are at stages 2 and 3, as in *R. nigrita*, perhaps as fuel for mating flights (cf. Downes, in press). They visit flowers throughout adult life.

#### IV.17.2. *Ramphomyia ursinella* Say

One female was taken on *Dryas integrifolia* on 25.VI.1967. It had pollen on its cuticle, but none in the gut. Its ovarian follicles



were at stage 2.

IV.17.3. *Rhamphomyia hoeli* Frey\*

Between 10.VI and 24.VII.1967, 37 specimens were collected or observed or both in association with flowers. Those associated with the flowers of *Dryas integrifolia* accounted for 29 females over the entire period, of which 24 were dusted with pollen, and 6 males, all dusted with pollen, from 19.VI to 8.VII. Ten (7 females, 2 males, and 1 other) were seen on the petals beneath the overhanging filaments; 8 females were collected as they rested on the anthers and 2 females were noted actively imbibing nectar, with their heads well down between the stamens and the pistils so that only the tips of their abdomens were visible. Three specimens were taken from deep within the corolla tubes of *Pedicularis arctica* flowers between 19.VI and 29.VI (1 male, 2 females). The corollas were pulled out of the calyces, and the insects seen with their mouthparts close to the nectar. None of these specimens carried pollen.

Twenty-seven females were dissected, 2 had ovarian follicles at stage 1, 9 at stage 2, 12 at stage 3, and 4 at stage 4. There appeared to be two distinct ovarian cycles, the first took from 24.VI to 29.VI, and the second another 6 days, from 30.VI to 5.VII. From 10.VI until 24.VI, 4 females had follicles no more developed than stage 2, while on the 26.VI and 27.VI, 3 had follicles at stage 2, and 4 had them at stage 3. On 29.VI the first fly was collected with follicles at stage 4. On 30.VI 2 females were collected, one at each of stages 1 and 2, on 3.VII one each at stages 2 and 3, and on 4.VII, 1 at stage

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\* Previously *R. sp. nr. lamelliseta*.



2, 4 at stage 3, and 1 at stage 4. After this date all individuals had follicles at stages 3 and 4.

Dissections showed no pollen grains in any guts.

The many females with follicles at stage 3 may reflect the fuel requirements for the swarming behaviour in mating (cf. Downes, in press).

McAlpine (1965) collected a male imbibing nectar from *D. integrifolia*. He also noted a female attempting to take nectar from *Lesquerella arctica* and remarks that they feed in a similar manner to *R. filicauda*. Hocking (1968) collected these flies from *Cerastium alpinum*, *Saxifraga oppositifolia* and *D. integrifolia*.

#### IV.17.4. *Rhamphomyia* (*Dasyrhamphomyia*) *nigrita* Zetterstedt

Between 24.VI and 21.VII, 65 specimens were collected and observed. These came mainly from the flowers of *Dryas integrifolia* (24.VI-16.VII.1967) which accounted for 24 females, 20 of which were dusted with pollen; and 9 males of which 5 carried pollen; 20 others were observed but escaped. Six females and 5 males were seen imbibing nectar. On two occasions individuals were observed as they started feeding. They first projected their fore-tarsi between the stamens and pistils, down towards the nectaries, presumably to taste for nectar (*vide* Dethier, 1963: Ch. V). They then upended themselves, projecting their heads down into the nectaries, and began to feed and probe with their elongate proboscides at the nectaries around the flower. The insects were seen feeding in two positions, one with their hind tarsi gripping the pistils, ducked so that their nota came into contact with the anthers (6 observations); and *vice versa* with their hind tarsi





gripping the stamens so that they ducked with their nota touching the stigmas (5 observations). One was noted feeding through the filaments from the side. One individual was noted as it approached a flower of *D. integrifolia*; it made 4 passes at it, landed on a lower petal, probed at the filaments in an attempt to feed through them from the side (see above), unsuccessful, it crawled up onto the sexual parts of the flower and commenced to feed with its notum towards the stigmas, imbibing from different nectaries for 2 minutes. The majority of these insects were observed apparently motionless on the flowers. I noted one\* individual within the same flower for over 38 hours during a spell of bad weather. They may remain in the flowers after feeding in response to warmth and become torpid as the temperature drops. They assume any angle of repose within the flowers. During sunny weather 11 were observed in flowers with their bodies vertical, 4 head uppermost, 7 head down; 9 were sitting across their flowers, 5 to the right and 4 to the left (*cf. R. filicauda*).

Other flowers are visited by these flies. Three females were collected as they imbibed nectar from *Polygonum viviparum*, and 1 likewise from *Potentilla* sp. (probably *nivea*). Four males and one unsexed specimen were taken similarly on *Arnica alpina* at Gilman Camp.

Forty-four individuals were examined for pollen, and 37 were dusted. Two of those without pollen on them were from *P. viviparum*, which produces very little pollen, the other captured on the flowers of this plant carried pollen of undetermined origin. No pollen was

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\* Based on circumstantial evidence. The fly was not marked, but the flower was. This event took place just outside my tent.



found in the guts of males or females and no pollen eating activity was seen.

Twenty-five females were dissected, 6 had ovarian follicles at stage 1, 13 at stage 2, 3 at stage 3, 2 at stage 4, and 1 was found on 19.VII without follicles and was assumed to be spent. Before 8.VII only stage 1 and 2 follicles were found, accounting for 16 observations. After this no stage 1 follicles were found. The many females at stage 2 may reflect their fuel requirements for mating and swarming behaviour happening at this stage of their lives (cf. Downes, in press).

Hocking (1968) reports that he captured a specimen of this fly with prey in a *D. integrifolia* flower in 1963. I have seen this only in *R. filicauda* and Downes (in press) records that *R. (D.) nigrita* captures its prey in flight.

#### IV.17.5. *Rhamphomyia* Spp.

Observations were made of 22 specimens which escaped. Of these 20 were in *D. integrifolia* flowers, 1 was in *Lesquerella arctica* (2.VII) with its notum against the stigmas, and the other was prey of *Xysticus deichmanni* on *Arnica alpina* (21.VII, Gilman Camp). Hocking (1968) records these flies on *Saxifraga tricuspidata*, *Potentilla* sp., and *Taraxacum* sp.

#### IV.18. *Syrphidae*

In general the Syrphidae are well known flower visitors, and may feed on nectar or pollen, or both (Müller, 1873). Müller (p. 35-36) gives a detailed description of pollen feeding by these animals, but they do not chew pollen (Faegri and van der Pijl, 1966: 86) nor do they triturate pollen grains into a "porridge" (Elton, 1966: 267);



rather, as Müller wrote, they rub a mass of pollen down so that the grains are united into a long thread which comes to lie in the groove of the labium, this is then thrust back into the mouth and the pollen grains are ingested whole. Oldroyd (1964: 157) completely neglects pollen feeding by Syrphidae, and discounts the need for any protein in their adult diets. He says "The adults have totally abandoned any carnivorous diet that their ancestors may have had, and have no piercing and crushing mouthparts. They now live entirely on nectar and honey-dew, which they suck up through the sponge-like labella of the labium. In this family protein-feeding has been relegated to the larval stage,..." This is not entirely correct; in many pollen has been substituted for flesh for dietary protein requirements.

A few observations of Syrphidae visiting flowers in the arctic have been made (Hartz, 1895 (*Salix arctica*; *Potentilla nivea*); McAlpine, 1965; Hocking, 1968; MacInnes, pers. comm. ; Chernov, 1963; 1966). Around Hazen Camp there are 4 species of Syrphidae, *Phalacrodira nigropilosa* (Curran), *Carposcalis carinata* (Curran), *Metasyrphus chillcotti* Fluke, *Helophilus borealis* Staeg. (Oliver, 1963).

#### IV.18.1. *Carposcalis carinata* (Curran)

Between 1.VI and 12.VII.1967, 68 specimens were collected or observed on flowers. Nineteen were seen in association with *Saxifraga oppositifolia* flowers between 1.VI and 15.VI (6 females from 7.VI-15.VI (4 females on 10.VI); 10 males, 2 on 1.VI and 8 on 10.VI; and 3 unsexed on 10.VI). Two of the males collected on 10.VI were the prey of a penultimate male of *Xysticus deichmanni*. All 16 specimens





collected had pollen externally, and all 12 dissected (6 males and 6 females) had pollen in their guts. On 10.VI, 1 male and 1 female were collected on *Erysium Pallasii*, both had ingested a little pollen and were observed with their feet on the petals and their labella appressed to the anthers. On 13.VI, 1 male was found feeding on the nectar of a pistillate catkin of *Salix arctica*. Between 8.VI and 12.VI, 18 (4 females, 9 males, 5 unsexed) were taken from staminate catkins of *S. arctica* (1 female, 5 males, and 5 unsexed on 10.VI). All those dissected contained pollen (7 males, 3 females), and all those examined were well dusted (8 males, 4 females, and 1 other), particularly on their heads and eyes. One individual (10.VI) hovered in front of 5 anthesed catkins, one after another without settling; I disturbed it at the 5th catkin. Between 16.VI and 22.VII, 25 specimens (7 males from 16.VI-20.VI; 18 females from 20.VI-22.VII) were collected and observed on *Dryas integrifolia* flowers. All the males were dusted with, and had ingested, pollen grains. Fifteen females had ingested pollen grains, but the other 3 had not; 16 were dusted, while 2 appeared clean. On 21.VI one female was collected on *Papaver radicatum*, on 9.VII, 1 male was taken on *Potentilla* sp. (probably *nivea*) and on 19.VI, 1 female was collected on *Lesquerella arctica*; all had ingested pollen grains.

McAlpine (1965) records *C. carinata* feeding on pollen grains of *D. integrifolia*, *Erigeron compositus*, *S. arctica*, *Potentilla nivea*, and imbibing nectar from *P. nivea*. Hocking (1968) records this syrphid from the inflorescences of female *Salix arctica*, *P. radicatum*, *Saxifraga oppositifolia*, *S. tricuspidata*, and *D. integrifolia*, on which 4 females

Note: The collection from 10.VI.1967 came from N1, 2 to J 4,5 in the foothill area of Mt. McGill associated with the first fault line (see Fig. 3).



were feeding on pollen.

From my data (1967) males dominated the collections 22 to 10 until 20.VI; after which the ratio became reversed at 7 males to 20 females. Hocking's first catch (3.VII.1963) of this species was of 2 males, after which all but 1, unsexed, were females. Twenty-eight females were dissected and their ovarian follicles examined for maturation stages; 7 showed stage 1, 10 stage 2, 4 stage 3, and 7 stage 4. The first female (8.VI) had follicles at stage 1, and 6 of those collected on 10.VI had stage 2 follicles. None was found with follicles as advanced as stage 3 until 20.VI, when 3 were collected together with 5 less mature specimens. The next day (21.VI) the first individual with fully ripe follicles was collected on flowers, and from that day on all those collected had follicles at stage 4 or late stage 3. It seems that the males emerge earlier than the females, and commence feeding on protein for spermatogenesis. The females may not emerge until the males are ready to mate, and then begin feeding on protein themselves for ovarian maturation. The females eat pollen at all stages of their adult lives. The higher incidence of females with follicles at stage 2 feeding on flowers may have significance in that after this stage yolk is deposited in the follicles. Digestion of the protein rich protoplast of the pollen grains must be by diffusion through the micropylar membrane, as pollen grains examined from the guts of these insects were unbroken (cf. Collembola; *Pogonomyoides segnis*; *Bombus*; other Syrphidae).

McAlpine (1965) describes how *C. carinata* feeds on the pollen of *D. integrifolia*. "To eat pollen the flies rested on the flowers, grasped one filament after another with their front tarsi and pulled the anthers to their mouths; their mouthparts are extremely flexible



and the labella were moved about freely in all directions as they fed. It is noteworthy that on several occasions single flies were observed taking pollen from one plant, e.g. *Dryas*, and then moving to a flower of *Potentilla* and taking nectar." The 2 I observed on *Erysium Pallasii* did not bring their fore tarsi into play.

IV.18.2. *Phalacrodira nigropilosa* (Curran)

Between 30.V.1967 and 15.VI, 31 specimens were collected.

Nineteen were taken in association with *Saxifraga oppositifolia* from 30.V to 9.VI. Of these, 11 (3 males and 8 females) had been killed and eaten by *Scatophaga apicaulis*, 31.V and 1.VI. On 7.VI, 1 was found killed and eaten by a spider (probably *Tarentula exasperans*). The remaining 7 (5 males and 2 females) were collected directly from the flowers; 3 of them were feeding on nectar, 1 visited several flowers before I captured it. When visiting flowers they hover momentarily in front before alighting and commencing to feed. Six of the 7 above were dusted with pollen, particularly on the head and eyes, the latter being covered with short hairs. Four (2 males and 2 females) of 5 dissected had pollen in their guts. Twelve specimens were taken in association with *Salix arctica* catkins from 3.VI to 15.VI. Of these 3 females were collected on pistillate catkins (9.VI-15.VI), 2 of which were dusted with pollen. One male was observed feeding on nectar of a pistillate catkin, it too was dusted with pollen. Of the 8 (4 males and 4 females) collected from staminate catkins of *S. arctica* (3.VI-9.VI), 2 (1 male and 1 female) were the prey of 2 males of *S. apicaulis* (3.VI and 7.VI). The remainder were dusted with pollen, and of 4 dissected (2 males and 2 females) all had pollen in their guts.





McAlpine (1965) records 2 males on *S. arctica*, one was eating pollen. Hocking (1968) records 1 male and 1 female on *Dryas integrifolia*.

Three females were dissected for ovarian follicle development between 8.VI and 9.VI, two had follicles at stage 1, and 1 was at late stage 3. It is probable that these flies visit flowers at all stages of their adult life. There does not appear to be a shift in the sex ratio as was noted for *Carposcalis carinata*.

#### IV.18.3. *Metasyrphus chillcotti* Fluke

Nine specimens were observed on flowers or collected or both between 3.VI and 27.VI. Three of these were observed on *Saxifraga oppositifolia*. One was watched as it probed with its labellum at the opened anthers of the flower it was visiting, its fore tarsi were not brought into play. The other two (1 male and 1 female) were collected; the gut of the male was distended with pollen. The male was dusted with pollen; and his gut was distended with pollen; the female had no pollen internally or externally, she appeared to be resting, moving only slightly with no movement of the mouthparts. Between 9.VI and 27.VI 1 male and 4 females were observed on *Salix arctica*. The male, collected from a staminate catkin was liberally dusted with pollen, but had ingested none (9.VI). Two females taken from pistillate catkins were dusted with pollen, as were the 2 collected on staminate catkins. One female was dissected and had ovarioles at stage 3 and had ingested pollen. On 25.VI, 1 male was collected from *Dryas integrifolia*, it had a little pollen in its gut, but was liberally dusted.

Neither Hocking (1968) or McAlpine (1965) record this fly from flowers.



IV.18.4. *Helophilus borealis* Staeg.

Three specimens were collected or observed on flowers. On 26.VI. 1967 one male was seen feeding on the nectar of *Dryas integrifolia*. On 5.VII an unsexed specimen was seen feeding on the nectar of *Dryas integrifolia*. It flew directly to the centres of the flowers from distances of up to 0.5 m and immediately started probing for nectar. It did not hover in front of the flowers before alighting, as did *P. nigropilosa* or *C. carinata*. When feeding it stood on the flower oriented vertically with its head uppermost, it then ducked its head between the gynoecium and androecium, from to the androecium, projecting its labella down to the nectaries. In this position it fed for about 10 seconds, probing with its labella as many of the nectaries as it could reach. Its fore tarsi gripped the stamens ahead of it, while the other pairs of legs gripped the gynoecium. On 18.VII.1967 a female was observed on *Arnica alpina* in the vicinity of Gilman Camp. It went from disc floret to disc floret, inserting its mouthparts deeply imbibing nectar. When it was dissected its gut was devoid of pollen, but distended slightly with clear syrupy fluid assumed to be nectar. Its ovarian follicles were at stage 4. Pollen was liberally dusted all over the underside of its abdomen. That day many individuals were seen around ponds, flying back and forth along a limited shore line, where they probably breed (*cf.* Coe, 1953).

Hocking (1968) records 3 females of *Helophilus borealis* visiting flowers, 1 from a male *Salix arctica* catkin, and 2 from *D. integrifolia*, the latter feeding on pollen. MacInnes (*pers. comm.*) has recorded *H. borealis* and *H. groenlandicus* (Fabr.) evidently seeking



nectar from *Pedicularis sudetica* Willd. "They enter the flower from the right to the left and push their head into the base of the galea. ...In this position the stigma of *P. sudetica* touches the left dorsal surface of the thorax which is where the pollen is most heavily dumped." These observations from McConnell River (60° 50' N., 94° 25' W.) in the low arctic.

#### IV.19. Piophilidae

Piophilids are not noted anthophiles. Chernov (1966) says that they are encountered fairly often, particularly *Piophila vulgaris* Flhn. on certain tundra flowers. I collected 1 female of *Allopiophila fulviceps* Holmgren (30.VI.1967) and 1 specimen of *Lasiopiophila pilosa* Staeger (17.VII.1967) on flowers of *Dryas integrifolia*. McAlpine (1965) also records a single female of *L. pilosa* imbibing nectar from *Dryas integrifolia* on 24.VI.1962. It had forced its head down between the stamens and had "inserted its fleshy labella into the droplets of nectar on the nectaries." A few grains of pollen were caught among its setae. On the same day McAlpine observed and collected 5 females of *Allopiophila arctica* Holmgren in the same species of flower imbibing nectar as is described above. These insects are less hairy and consequently had scarcely any pollen adhering to them. Hocking (1968) collected 1 male and 2 females of the latter species, 1 of each sex on male *Salix arctica* catkins and 1 on *D. integrifolia*.

#### IV.20. Agromyzidae

*Phytomyza erigerontophaga* Spencer was collected on four occasions, and observed on one other between 9.VII and 16.VII on the inflorescences of *Erigeron compositus*, one of its host plants (Spencer, 1970). Their





activity is unknown, they were always found on the disc florets. Those dissected, 1 male and 1 female, and those examined for taxonomic purposes, 1 female and 3 males by V. K. Sehgal were devoid of pollen internally and externally. On 7.VII.1968 a pair was collected in copula from the disc florets of the above plant. The flowers may serve as a source of nectar, and possibly as a site for bringing the sexes together.

These insects were not found on *E. eriocephalus* or *Chrysanthemum integrifolium*. McAlpine (1965) records *Phytomyza* sp. visiting a flower of *Dryas integrifolia*. I recorded one specimen of *Phytomyza* sp. prob. *erigerontophaga* (G.E. Shewell, pers. comm.) from *Potentilla* sp. prob. *nivea* at Gilman Camp on 15.VII.1967. Its head was down and the mouthparts appeared to be in the nectar which I assume it was imbibing. It was dusted with pollen on its head, particularly the labella; thorax, and abdomen. It had ingested no pollen grains.

#### IV.21. Calliphoridae

Calliphorids have been reported visiting the flowers of numerous families (Müller, 1873; Knuth, 1906-1909) and are well known anthophiles in the arctic (McAlpine, 1965; Chernov, 1966). At Hazen Camp there are three species -- *Protophormia terraenovae* (Robineau-Desvoidy), *Boreellus atriceps* (Zetterstedt), and *Protocalliphora sapphira*.

##### IV.21.1. *Protophormia terraenovae* (Robineau-Desvoidy)

On 1.VI.1967, 1 male was collected feeding on the nectar of a pistillate catkin of *Salix arctica*. In 1966, 2 males were collected feeding on the nectar of *Saxifraga oppositifolia*. No further confirmed records were made, because, as McAlpine (1965) points out, they become



more interested in the observer than in the flowers they visit, and are difficult to catch. Nevertheless, McAlpine (*op. cit.*) saw many visiting the catkins of *S. arctica*, and remarks that every specimen he collected in 1962 was "heavily laden with (willow?) pollen." Hocking (1968) observed two females taking nectar from male willow catkins, 1 feeding on female willow catkin, and 1 on each of *D. integrifolia* and *Cassiope tetragona* with uncertain activity. Both McAlpine and Hocking relied on field identifications of uncollected material, I was unable to distinguish *P. terraenovae* from *B. atriceps* without capturing the specimens.

IV.21.2. *Boreellus atriceps* (Zetterstedt).

*B. atriceps* was collected from flowers from 25.V.1967 (the first day any flowers were seen) until 19.VII. Nineteen females and 18 males were collected from *Saxifraga oppositifolia* between 25.V and 8.VI; of these 30 were noted to be feeding on nectar, which they did with great vigour. Several were observed as they approached the flowers, flying straight to them from as much as 0.5 m distant. They landed without hesitation, and projected their fore tarsi into the flower, presumably to taste for sugar (Dethier, 1963: Ch. V) before they upended themselves into the corolla so that only the abdomen and hind legs were visible to feed. Of the 13 males examined for external pollen grains, 6 carried them mainly on their eyes and heads; whereas of the 15 females examined, only 2 had pollen on them.

On 8.VI and 9.VI, 8 (3 males and 5 females) were collected as they fed on the nectar of staminate catkins of *Salix arctica*, 2 males and 2 females were collected from unsexed catkins of *S. arctica*.



None carried pollen. Three females were collected from *D. integrifolia* (2,28.VI; 1,10.VII): all were dusted with pollen, the last mentioned specimen had pollen grains on its mouthparts, but had not ingested any. On 14.VII and 19.VII, 1 female was collected from each of *Arnica alpina* and *Taraxacum* (prob. *arctogenum*), and both carried pollen grains. At Gilman Camp on 18.VII one female was watched as it fed at *A. alpina*. It dipped its head several times inserting its labella into disc florets. It was dusted with pollen on its calypters.

On 19.VI.1962 McAlpine (1965) observed 4 females of this species from *Potentilla nivea* flowers, where they were feeding on nectar. These flies stood astride the flowers with their labella against the nectaries, they "revolved around each flower pausing momentarily as the labella were pressed against each nectary. While doing this the palpi were extended forward at right angles to the main axis of the proboscis. As the fly finished imbibing nectar from each nectary, it frequently "licked" the base of the petal in a manner reminiscent of a dog licking a plate." One female was seen to visit 8 flowers in this way in 2 minutes. Hocking (1968) records 1 on *Saxifraga oppositifolia* and 2 females from *D. integrifolia*.

McAlpine (1965) records that these flies, especially the females, were frequently heavily dusted with pollen. The difference between these findings and my own is inexplicable. Fifty-one were dissected, and none found to have ingested any pollen grains.

These flies must overwinter as adults, for they are evident in abundance almost as soon as the snow leaves the ground. On 15.VI. 1968 they were first seen flying around at the snout of Per Ardua glacier, where most of the ground was still well covered with snow.





Several of the early collected specimens from Lake Hazen in 1967 had battered and frayed wing margins, no evident body fat, and some females were noted to have ovarian follicles at stage 4. They are the first flies to become active after the winter, and are the first to feed on the first flowers. Females collected on flowers showed all stages of follicular development; 3 were collected with stage 1 follicles, 2 at stage 2, 2 at stage 3, 7 at stage 4, and 1 spent. The significance of the higher number at stage 4 may lie in the greater weight of the fly, therefore requiring more fuel to fly, or it may lie in the necessity for the fly to hunt out a site for oviposition, again requiring fuel for flight, or both.

#### IV.21.3. *Protocalliphora sapphira*

This fly breeds in birds nests. In 1968, 4 pupal cases, assumed to belong to this species were found in an abandoned nest of the snow-bunting (*Plectrophenax n. nivalis*). It was never collected in flowers, although it is likely to be a nectar feeding species.

#### IV.21.4. Calliphoridae Spp.

These unidentified flies account for over 90 observations between 31.V and 17.VII. More than 50 specimens were observed on *S. oppositifolia* feeding on nectar between 31.V and 13.VI. One individual was observed (1.VI) as it visited 7 flowers consecutively, flying straight from one to another and alighting without the slightest hesitation before feeding as described above for *Boreellus atriceps*. Between 9.VI and 31.VI, 9 were observed on staminate catkins of *S. arctica* feeding on nectar with their heads well in amongst the anthers. One individual was watched as it visited 2 catkins flying straight from one to the



other, landing without hesitation and feeding; another was seen to walk 15 cm up to a catkin, climb up the stem and onto the inflorescence to feed with its head pushed well amongst the florets. How these can fail to pick up pollen is inexplicable. Two observations were made of these insects feeding on the nectar of pistillate catkins of *S. arctica* (2.VI and 12.VI). At Gilman Camp between 16-19.VII, 28 specimens were seen on *Arnica alpina*, presumably feeding on nectar.

#### IV.22. Tachinidae

Oliver's (1963) list is incomplete. There are at least 4 species around Lake Hazen. Tachinidae are known to visit flowers in the arctic (Chernov, 1966).

##### IV.22.1. *Pectinartica stylata* (B. and B.)

I collected one female as it imbibed nectar from a pistillate catkin of *Salix arctica* on 9.VI.1967. It carried no pollen, had none in its gut, and had ovarian follicles at stage 3. Hocking (1968) records 2 individuals on flowers.

##### IV.22.2. *Periscepsia* n. sp.

I collected 1 male on 20.VI. It visited a flower of *Saxifraga oppositifolia* and a pistillate catkin of *Salix arctica*. It carried a little pollen. On 28.VI I collected a female from a flower of *Dryas integrifolia*. It was dusted with pollen, but had ingested none. Its ovarian follicles were at stage 3.

##### IV.22.3. *Murdockiana gelida* (Coquillett)

McAlpine (1965) recorded a single male apparently eating pollen of *Dryas integrifolia*.



IV.22.4. *Peleteria aenea* Staeger

Between 14.VII and 26.VII.1967, 18 (12 males, 6 females) of these insects were collected from flowers. Four males (16.VII; 17.VII; 2, 18.VII) were collected as they visited inflorescences of *Arnica alpina*; one (16.VII) was watched as it flew directly over 1 meter from one inflorescence to another where it landed on the disc florets and fed; another (18.VII) did exactly the same thing, but over a shorter distance. Once on the disc it walked about ducking its head and inserting its mouthparts into floret after floret to imbibe nectar, as did also that of 17.VII. Of the 3 examined 2 carried pollen grains, particularly on their venters, none had ingested any. Three females (2, 14.VII; 16.VII) were collected on *A. alpina* discs. All were dusted with pollen, but had ingested none and had ovarian follicles late in stage 3. Only 1 was seen feeding on nectar as described above; it fed from 3 disc florets before I caught it. They oriented vertically on the flowers, (1 head uppermost and 2 head down). At Hazen Camp, 2 males (16.VII, 17.VII) were watched as they walked around the flowers of *Dryas integrifolia* imbibing nectar. They showed no fixed pattern of behaviour but managed to stay almost free of pollen grains. Another male (16.VII) was watched behaving exactly as above on *Potentilla nivea*. On 19.VII a single male was watched as it visited 4 flowers of *Stellaria longipes* before it was caught. It spent about 5 seconds at each flower, walking rapidly around imbibing nectar; it was well dusted with pollen. On the same day (19.VII) 3 males were collected from spikes of *Polygonum viviparum* upon which they oriented vertically, head down, moving from flower to flower to imbibe the nectar; one was well dusted with pollen, one had none, and the other had only its





venter dusted. On 21.VI a single male was collected from *P. viviparum*.

The remaining 3 females were collected at Hazen Camp. One (26.VI) from *Lesquerella arctica* was watched as it flew from flower to flower presumably imbibing nectar, although its labella were well dusted with pollen grains. It was not dissected. One (16.VII) was watched as it walked rapidly all over a flower of *Dryas integrifolia*; the insect was well dusted with pollen, but had ingested none, the ovarian follicles were at late stage 3. The last (19.VII) was taken on a spike of *P. viviparum* as it imbibed nectar. It was covered with pollen, had ingested none, and had ovarian follicles at stage 3.

*Peleteria* spp. (*Peleteria adelphe* Zim. and *P. nigricornis* R.-D.) are noted by Chernov (1966) from flowers of *Dryas punctata* Juz., and *D. octopetala* L.

#### IV.22.5. Tachinidae Spp.

This group of observations was made on Tachinids which escaped. Many were no doubt *P. aenea*. Seventeen were seen on *Arnica alpina* at Gilman Camp between 13.VII and 19.VII; 2 of these were watched as they visited 3 inflorescences each flying directly from disc to disc where they walked rapidly about ducking their heads and inserting their mouthparts into florets. One was noted to keep to the edge of the disc, which, on examination, was the only area of open florets. Two (11.VII; 17.VII) were watched imbibing nectar from *Dryas integrifolia* and two (16.VII; 17.VII) on *Potentilla nivea* as described for *P. aenea*. One other (8.VII) was seen on an inflorescence of *Taraxacum arctogenum* but its activity was not determined.



IV.23. Cordylurinae (Scatophaginae) (Muscidae)

Generally the Cordylurinae are predatory on smaller insects (Hobby, 1931) but are known to visit flowers. Müller (1873) records species of *Scatophaga* from flowers of 9 families. At Hazen Camp three species of *Scatophaga* are known, *S. apicaulis* Curt., *S. multisetosa* Holmgr., and *S. nigripalpis* Beck.

IV.23.1. *Scatophaga apicaulis* Curt.

Twenty-six (13 males, 6 females, 7 unsexed) specimens of *S. apicaulis* were collected between 31.V and 12.VI. Three males, 2 females, and 4 unsexed were taken from *S. arctica* (6 from staminate catkins, 3 from pistillate). Four of these (2 males, 2 unsexed) were observed taking nectar from both male and female catkins. Three were seen preying; 1 female on a female *S. arctica* catkin was eating *Nematus* sp. (12.VI); 2 (1 male) (3.VI and 7.VI) on male catkins were eating *Phalacrodira nigropilosa* (1 female, 1 unsexed). Between 31.V and 3.VI, 5 females, 10 males, and 1 other were observed feeding on nectar, with their heads well down into the corollas of *Saxifraga oppositifolia*. Two pairs were seen mating. Two females and 2 males were seen merely resting on the flowers, although they could have been awaiting prey, as 3 specimens (1 male, 2 unsexed) were seen feeding on *P. nigropilosa* during the same period (31.V and 1.VI). Beneath the flowers in which two of the above were captured there were piles of *P. nigropilosa* corpses, all female. One *S. apicaulis* had consumed two, and was in the process of eating a third, while the other had eaten two but was without prey when caught, the third was in the process of eating, but there were no corpses beneath its flower. One female was collected as it rested on a flower of *Dryas integrifolia*



on 31.VIII.1967. Its tarsi gripped the anthers. It was well dusted with pollen but had none in its guts. Its ovaries were spent. Dissections revealed no pollen in their guts, and there is no reason to suspect that this species was eating pollen. Though hairy, only three specimens had pollen externally.

IV.23.2. *Scatophaga multisetosa* Holmgr.

On 8.VI.1967 one female specimen of *S. multisetosa* was collected from a staminate catkin of *Salix arctica*.

IV.23.3. *Scatophaga* Spp. or Sp.\*

On 31.VI 3 *Scatophaga* spp. or sp. were watched as they took nectar from *S. oppositifolia*. On 2.VII, 2 specimens were noted similarly engaged on *Taraxacum* sp. (prob. *arctogenum*) in Skeleton Creek. None were captured.

IV.23.4. *Scatophaga nigripalpis* Beck.

McAlpine (1965) records a specimen of this insect feeding on *Dryas integrifolia* pollen. It was lapping at newly-opened anthers with its proboscis, and several thousand pollen grains remained adhering to its hairy body. Hocking (1968) reports seeing one specimen flying over *S. oppositifolia*.

IV.24. *Muscidae* (*Anthomyiinae*)

IV.24.1. *Fucellia pictipennis* Becker

This fly is very common at the beginning of the season, when

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\* Excludes *S. nigripalpis*.





large numbers of them run about the ground. Ten specimens were observed or collected or both from 2.VI until 12.VI.1967 on flowers. Two males, 1 female, and 4 which escaped were observed on *Saxifraga oppositifolia*; 2 were noted as imbibing nectar, which they did by clinging onto the filaments with their hind and mid tarsi so that their bodies were inverted between the stamens and pistils and their mouthparts applied to the droplets of nectar at the base of the corolla. None of those collected had pollen on them. Two males and 1 other were seen on *Salix arctica* catkins (staminate and pistillate), (8.VI and 9.VI) 1 was noted imbibing nectar with its head pushed well into the florets. Both those collected including one from a female catkin had been dusted with pollen. Hocking (1968) saw 1 individual on *S. oppositifolia*. McAlpine (1965) records 1 female imbibing the nectar of *Dryas integrifolia*, and describes how the fly landed on the center of the flower, and forced its head down towards the nectar between the outer row of stamens.

#### IV.24.2. *Pegomyia* Sp. or Spp.

Hocking (1968) records these flies on flowers. I collected one female *P. arctica* Ringd. on a flower of *Dryas integrifolia* on 30.VI; it was dusted with pollen, but had none in its guts. Its ovarian follicles were at stage 4, but only the left ovary was present. One female of *Pegomyia* sp. was taken from a flower of *D. integrifolia* at Gilman Camp on 17.VII, it was dusted with pollen. The specimen was mutilated and sucked dry by *Xysticus deichmanii*.



IV.25. Phaoniinae

IV.25.1. Eupogonomyia groenlandica (Lund.)

Thirteen specimens (5 males, 8 females) were collected from inflorescences. One female was taken from each of *Saxifraga oppositifolia* (15.VI), *Draba* sp. (19.VI), and a staminate catkin of *Salix arctica* (20.VI), the last was well dusted with pollen and had its head inserted into the catkin as was assumed to be imbibing nectar. Three females (1, 28.VI; 2, 4.VII) were collected from *Dryas integrifolia* flowers, 2 were dusted with pollen, 1 was clean, and the first mentioned specimen (28.VI) had eaten pollen grains. Three males were collected on *D. integrifolia* on 10.VII, 2 were dead from fungus disease caused by *Entomophthora muscae* (Fr.) (Fries.) (this fungus is widespread on muscoid flies in the arctic (Savile and Parmlee, 1964)). The live specimen was dusted with pollen. The same day, at Gilman Camp, 1 male without pollen was collected from a flower of *Potentilla nivea*. One female dusted with pollen was collected as it imbibed nectar from *P. nivea* at Gilman Camp on 8.VII. On 13.VII a female, with her notum dusted with pollen, was watched as she pushed her head under the pistil as if looking for nectar in *Papaver radicatum* at Gilman Camp. One male was collected from *Arnica alpina* where it had fallen prey to *Xysticus deichmannii* on 17.VII at Gilman Camp. Of the 2 males and 8 females dissected, only 1 female had eaten pollen. Ovarian follicular development ranged from stage 1 to stage 4 (Table 3).



Table 3.

Ovarian follicular development in *E. groenlandica* females visiting flowers around Hazen Camp in 1967.

<u>Date</u>	<u>No. Dissected</u>	<u>Follicular Stages</u>	<u>Comments</u>
15.VI	1	1	
19.VI	1	2	
20.VI	1	4	Large fat bodies present
28.VI	1	3	Pollen feeding
4.VII	2	2,4	
13.VII	1	4	
18.VII	1	4	

The apparent lack of males until the first week in July 1967 may not be important in that Hocking (1968) collected 2 males (of a total of 3 flies) on flowers in late June 1963.

IV.25.2. *Pogonomyoides segnis* of Hucket nec. Holmgren\*

Between 19.VI and 17.VII 19 females (20.VI to 17.VII) and 6 males (2, 19.VI; 20.VI; 26.VI; 30.VI; 5.VII) were collected from the flowers of *Dryas integrifolia*. Of the males all but one (20.VI) caught on an unanthesed flower were dusted with pollen, none had ingested pollen grains. Only 1 (5.VII) was noted imbibing nectar which it accomplished with its head between the androecium and gynoecium with its notum touching anthers so that it was covered with pollen; it fed from three sectors of the flower, at the 3 o'clock position for 20 seconds and for 5 seconds each at 6 o'clock and 9 o'clock. McAlpine (1965) recorded one male feeding on *D. integrifolia* nectar while it was on the petals and its head pushed through the filaments, in this way little pollen adhered to its body. The specimen collected on

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\* D. M. Wood (pers. comm.).





20.VI was basking. The activities of the remainder were not determined although the presence of pollen on their dorsa indicate that they had been imbibing nectar. One other male was collected dead from the fungus *Entomophthora muscae* on the apex of a spike of *Polygonum viviparum* on 19.VII.

Of the 19 females from flowers of *D. integrifolia* all but one (15.VII) were dusted with pollen. Two females were watched as they imbibed nectar; the first (16.VII) gripped the anthers and filaments with its tarsi and probed its head down between the androecium and gynoecium so that its dorsum touched the stigmas, it had pollen on its notum. The second (17.VII) fed with its dorsum in contact with the anthers and was well dusted with pollen on its notum and thorax generally. Two females were observed motionless on flowers, one oriented at 9 o'clock and one at 12 o'clock. Pollen feeding is common in females of this species (cf. McAlpine, 1963; and below) and I watched 2 females feeding on *D. integrifolia* pollen as described by McAlpine (1963), although I did not record their holding the filament of the stamen to which the anther they lapped with their labella belonged. Two other females (16.VII and 17.VII) were collected from *Potentilla nivea* flowers from which they imbibed nectar, both stood on the petals with their heads held well down through the stamens and their labella projected into the nectar. Only one (16.VII) carried pollen, then only on its face. One female (18.VII) was collected from an inflorescence of *Arnica alpina* at Gilman Camp, its activity was not determined, but it was well dusted with pollen.

Of 22 females dissected 15 had ingested pollen grains. The results of dissections showing follicular stages and pollen ingestion



are given with dates in Table 4.

It seems that the females upon emerging do not feed on pollen grains. The first specimens collected having one of large fat bodies, unexpanded wings, or stage 1 follicles, all indicating that these flies were very young. None had ingested pollen. Later, pollen is ingested as a source of nutrients for follicular maturation from stage 2 to 3 and 4 and for the second gonadotrophic cycle. McAlpine (1963) records 5 females ingesting pollen grains from 19.VI to 24.VI.1962, but no hint of their ages is given. Certainly Hocking's (1968) two records of pollen in the guts of females collected on 25.VII.1963 fall within the period when pollen feeding is expected.

Males appear to be more abundant on flowers early in the season, perhaps because roughly synchronously after emerging they require fuel to spend a search of mates. After this time individuals visit flowers for further fuel as the need arises.

#### IV.25.3. *P. segnis* or *E. groenlandica*

A single female collected from a flower of *Dryas integrifolia* on 4.VII was dusted with and had ingested pollen grains. Her ovarian follicles were at stage 4. The data collected on this specimen make it likely to be *P. segnis*.

#### IV.26. *Limnophorinae*

Holmgren (1869) recorded several species of *Spilogona* under the generic name *Aricia* as flower visitors in the arctic. Subsequent workers (McAlpine, 1965; Mosquin and Martin, 1967; Hocking, 1968) have added more observations.



Table 4.

Pollen ingestion and ovarian follicular development in female *P. segnis* throughout the 1967 season at Hazen Camp.

<u>Date</u>	<u>Number</u>	<u>Follicular stage</u>	<u>Pollen ingested</u>	<u>Comments, notes</u>
20.VI	1	2	no	Fat bodies large, wings not frayed
26.VI	1	1	no	
	1	2	no	Wings unexpanded
28.VI	5	2	yes	
	1	2	no	
	1	3	yes	Watched while ingesting pollen
	1	4	yes	Watched while ingesting pollen, nulliparous
	1	?	no	A little fat present
4.VII	1	4	yes	<i>P. segnis</i> or <i>E. groenlandica</i>
12.VII	1	?	yes	abdomen crushed
15.VII	1	?	(no)	2 imbibing nectar, 2 late stage 3
16.VII	3	3	yes	nulliparous? A little fat present
	1	4	no	2 imbibing nectar
17.VII	3	4	yes	early stage 3, ovaries with much tracheation
18.VII	1	3	yes	
19.VI	2 males			
20.VI	1 male			
26.VI	1 male			
30.VI	1 male			
5.VII	1 male			
19.VII	1 male			





IV.26.1. *Spilogona almquisti* Holmgr.

Hocking (1969) records one female from *Dryas integrifolia*.  
Mosquin and Martin (1967) record this fly from *Arnica alpina* on  
Melville Island.

IV.26.2. *Spilogona deflorata* Holmgr.

One male was taken from *Dryas integrifolia* by Hocking (1968).

IV.26.3. *Spilogona denudata* Holmgr.

Holmgren (1869) recorded this fly from flowers of *Cerastium alpinum*. I found one male of this species (5.VII) and one other possibly of this species (26.VI) were taken from flowers of *Dryas integrifolia*. Both were dusted with pollen, but neither had ingested any. The first specimen (5.VII) was watched as it imbibed nectar from four positions on its flower, the first two it gripped the stamens and upended itself so that its dorsum touched the stigmas, the second 2 times it gripped the pistils so that its dorsum touched the anthers. One female (30.VI) was also collected from a flower of *D. integrifolia*, it was dusted with pollen, had ingested none and had ovarian follicles at stage 3.

IV.26.4. *Spilogona dorsata* Zett.

Holmgren (1869) recorded this fly from flowers of *Cerastium alpinum*. One female *S. dorsata* or *S. tundrae* was collected from a flower of *Dryas integrifolia* on 12.VII. It was dusted with pollen and had ovarian follicles at stage 4.

IV.26.5. *Spilogona extensa* Mall.

One female possibly of this species was collected on a flower of



*Dryas integrifolia* on 10.VII. It was not dusted with pollen.

IV.26.6. *Spilogona latilamina* Collin.

Three females probably of this species (30.VI; 2, 10.VII) were collected from flowers of *Dryas integrifolia*, all were dusted with pollen, none had ingested any, and all had ovarian follicles at stage 4.

IV.26.7. *Spilogona melanosoma* Huck.

Fourteen specimens were collected from flowers between 26.VI and 20.VII.1967. Three males (26.VI; 30.VI; 5.VII) were collected from flowers of *Dryas integrifolia*, all were dusted with pollen, none had ingested any; one (5.VII) was watched imbibing nectar as it gripped the stamens with its tarsi and ducked so that its dorsum touched the stigmas. One other male (20.VII) was collected from a flower of *Stellaria longipes* at Gilman Camp where it ducked several times to feed on nectar. One female (5.VII) was found dead, sucked dry, in a cobweb across a flower of *D. integrifolia*, no spider was seen but it was likely *Dictyna borealis*. The remaining 9 females were all on flowers of *D. integrifolia*, all were dusted with pollen, but had none in their guts. Three were observed as they imbibed nectar, 2 (30.VI; 5.VII) gripped the pistils with their tarsi and ducked so that their dorsa touched the anthers, the other (5.VII) gripped the filaments between which it pushed its mouthparts to feed so that its dorsum was directed to the petals. Table 5 shows the follicular stages with time.

Table 5.

Ovarian follicular development in *S. melanosoma* visiting flowers around Hazen Camp in 1967.

<u>Date</u>	<u>Number</u>	<u>Stage</u>
30.VI	2	3
	1	4
2.VII	1	3
5.VII	3	4
10.VII	2	4



It appears that the females of this fly visit flowers for nectar mainly when they are almost ready to lay their eggs at which time they would require energy for hunting out oviposition sites or mating. Too few males were collected to comment on.

Hocking (1968) recorded *S. melanosoma* from flowers in 1963.

IV.26.8. *Spilogona obsoleta* Mall.

One male specimen possibly belonging to this species was collected from a flower of *Dryas integrifolia* on 27.VI. It was dusted with pollen but had ingested none.

IV.26.9. *Spilogona sanctipauli* Mall.

Both McAlpine (1965) and Hocking (1968) saw *S. sanctipauli* on flowers. I recorded 19 specimens of this species and a further 21 probably belonging to it. Of the males 26 were collected from flowers of *Dryas integrifolia* (8, 28.VI; 1, 27.VI; 1, 26.VI; 2, 30.VI; 1, 3.VII; 4, 5.VII; 2, 10.VII; 4, 12.VII; 1, 17.VII). All but one (5.VII) were dusted with pollen, none had any in their guts. Five males were watched as they imbibed nectar; one (5.VII) was watched as it fed 4 times at the same flower, twice gripping the filaments and ducking so that its dorsum touched the stigmas after which it ducked twice gripping the pistils so that its dorsum touched the anthers; two others (5.VII) imbibed nectar in the first position described; another (3.VII) imbibed nectar gripping the filaments and its head pushed between them so that its dorsum faced the petals exactly as McAlpine (1965) describes for the same species. One male (5.VII) was regarded as basking, but another (17.VII) in a similar position but in a shaded flower was regarded as resting. Two males (13.VII at Gilman





Camp and 17.VII) were collected from flowers of *Papaver radicatum*, only the former carried pollen, the latter rested on a petal; two other flies resembling *S. sanctipauli* escaped from *P. radicatum* at my approach (13.VII, Gilman Camp). One male (19.VII) was collected apparently imbibing nectar from the flowers at the apex of a spike of *Polygonum viviparum*, it carried very few pollen grains. None of the males had pollen in their guts.

All eleven females (7, 28.VI; 1, 30.VI; 1, 2.VII; 2, 5.VII) were collected on flowers of *D. integrifolia*. All were dusted with pollen, and none had ingested any. Two (5.VII) were watched as they imbibed nectar as described for the males (5.VII), one had its dorsum touching the stigmas, and the other the reverse; the latter fed in two sectors, at 3 o'clock and at 9 o'clock for 30 seconds and 15 seconds respectively. One (30.VI) was watched sitting motionless on a flower for several seconds before it was caught. Table 6 shows the ovarian follicle stages with time.

Table 6.

Ovarian follicular development in *S. sanctipauli* visiting flowers around Hazen Camp in 1967.

<u>Date</u>	<u>Number</u>	<u>Stage</u>
28.VI	2	2
	1	3
	3	4
30.VI	1	4
2.VII	1	3
5.VII	2	4

It appears that the females of this fly visit flowers mainly when they are almost ready to oviposit, at which time they would



require energy for searching out oviposition sites or mating (cf. *S. melanosoma*). The large number of males taken on flowers may reflect nutritional needs for mating flights as well as convenient places to bask or perhaps await the females.

Mosquin and Martin (1967) record this fly from *Arnica alpina*.

IV.26.10. *Spilogona torensis* Ringd.

One female was collected from a flower of *Dryas integrifolia* on 30.VI. It was dusted with pollen, but had ingested none. Its ovarian follicles were at stage 2; there were few follicles and the insect assumed parous.

IV.26.11. *Spilogona tundrae*

Two males (10.VI; 5.VII), 2 females (30.VI) as well as 1 female probably of this species (27.VI) and 1 *S. tundrae* or *S. dorsata* (12.VII) (see *S. dorsata*) were collected from flowers of *Dryas integrifolia*. All but 1 female (30.VI) were dusted with pollen, none had any in their guts. One male (10.VI) was watched as he imbibed nectar, gripping the pistils with his tarsi he ducked so that his dorsum touched the anthers. Two (1 male, 5.VII; 1 female, 30.VI) were considered basking. Of the females one (27.VI) had ovarian follicles at stage 2, one (30.VI) at late stage 3, one (30.VI) at stage 4 and nulliparous, and the last (12.VII) at stage 4 but parous.

IV.27. *Muscidae* (excluding *Scatopaga* spp.)

Muscidae are very alert and difficult to catch. I made many notes on specimens which escaped and were thought to belong to the Phaoniinae, Anthomyiinae, and particularly to *Spilogona* sp. Twenty-eight observations



are included here. Between 26.VI and 10.VII, 17 were recorded from flowers of *Dryas integrifolia*. On 26.VI one was watched as it flew back and forth in front of a flower about 2 cm from it, it landed on the gynoecium. On 30.VI, 3 specimens were watched basking within corollas and one female dusted with pollen, as she imbibed nectar. On 5.VII, 7 specimens were watched, 4 were basking and 3 imbibed nectar, all gripped the pistils with their tarsi and ducked so that their dorsa touched the anthers. On 9.VII, 2 were watched basking, and 1 imbibing nectar as above. On each of 8.VII and 17.VII a specimen was seen in flowers of *Papaver radicatum*, the former resting on the stigma; on 13.VII, 2 others were seen in flowers of *P. radicatum*.

At Gilman Camp between 13.VII and 21.VII, 11 insects were seen on inflorescences of *Arnica alpina*. On 13.VII one was watched as it approached an inflorescence, landing without hesitation on a ray floret from whence it walked on to the disc and began imbibing nectar. On 14.VII, one was watched imbibing nectar from the florets at the edge of the disc, these were the only ones open.

At Gilman Camp a male of *Spilogona* sp. and another muscid were collected from flowers of *D. integrifolia*, they carried no pollen and had been badly mutilated by *Xysticus deichmanni* (17.VII).

#### IV.28. Hymenoptera (Tenthredinidae)

Oliver (1963) lists only *Nematus* sp. as determined by W. R. M. Mason. Mason later identified *Amauronematus amentorum* (Forst.) and *Amauronematus* sp. from Hocking's collection of 1963.

Müller (1873) found Tenthredinidae very common visitors to the Umbelliferae, and *Salix* spp. He includes 5 species of *Nematus* in





his listings (p. 466).

IV.28.1. *Nematus* sp.

Between 3.VI.1967 and 28.VI.1967, 7 specimens of *Nematus* sp. were collected. Of these 5 (2 males, 1 female, 2 unsexed) were collected from pistillate catkins of *Salix arctica*; two males and one unsexed individual, the prey of a female of *Scatophaga apicaulis*, were caught on 12.VI, the female was collected on 19.VI, and the remaining unsexed specimen on 28.VI, the last specimen, although captured on a pistillate catkin was well dusted with pollen. On 9.VI a specimen was captured on a staminate catkin of *S. arctica*, its activity was not ascertained and it carried no pollen. The first specimen, 3.VI, was observed flying from flower to flower imbibing nectar as it dipped its head into the corollas of *Saxifraga oppositifolia*, it was well dusted with pollen under its thorax and on its head.

Since the larvae of *Nematus* sp. at Lake Hazen feed on *Salix arctica* catkins (Downes, 1964), it is likely that the female insects found on the female catkins were searching for oviposition sites. Only the individual taken from *S. oppositifolia* before *S. arctica* catkins were abundant was seen feeding, otherwise their activities are unknown. Furthermore, two types of eggs were found on female catkins, frequently larger yellow eggs (perhaps those of *Nematus* sp.) and rarely, smaller white sculptured eggs (perhaps those of the cecidomyid mentioned by Downes (1964). Males on catkins could be awaiting mates. It is significant that 4 of the 5 on catkins were on pistillate catkins. These provide more nutriment as the seeds develop than the male catkins which shrivel away after anthesis.



IV.28.2. *Amaurenematus amentorum* (Forst.)

Hocking (1968) recorded two females visiting flowers, one on each of *S. oppositifolia* and *Dryas integrifolia*. In neither case was their activity determined beyond resting.

IV.28.3. *Amaurenematus* sp.

Hocking (1968) recorded one female as possibly ovipositing on a female catkin of *Salix arctica*.

IV.29. *Hymenoptera: Apocrita*

IV.29.1. *Hymenoptera: Apocrita: Chalcidoidea*

IV.29.1.1. *Chalcidae*

Oliver (1963) lists one species, *Copidosoma* sp. Chalcids are not noted flower visitors. I collected 1 chalcid from a flower of *Saxifraga Hirculus* on 8.VII.1967 at Hazen Camp as it ran about the base of the corolla, it carried no pollen, and was accompanied by a specimen of *Stenomacrus* sp. (Ichneumonidae) in the same flower. At Gilman Camp 4 chalcids were collected from the flowers of *Stellaria longipes* on 20.VII.1967 as they appeared to feed on the nectar; their tarsi gripped the petals and their heads were directed to the nectar to which their mouthparts seemed to be applied. Hocking (1968) recorded 2 chalcids on *Potentilla* sp.

IV.29.1.2. *Eulophidae*

These are not recorded by Oliver (1963). I collected two specimens of *Tetrastichus* sp. from *S. longipes* on 20.VII.1967 at Gilman Camp in exactly the same circumstances as the chalcids (see above).

IV.29.1.3. *Pteromalidae*

This genus is not listed by Oliver (1963). Five specimens were collected from Gilman Camp on 20.VII.1967 from *Stellaria longipes*.



They appeared to be imbibing nectar as their heads were directed to the center of the flowers as they stood on the petals and sepals, and applied their mouthparts to the nectar.

IV.29.2. Hymenoptera: Apocrita: Ichneumonoidea

IV.29.2.1. Braconidae

Three genera are listed by Oliver (1963); *Apanteles* (3 spp.), *Aphidius* (1 sp.) and *Rogas* (1 sp.). Hocking (1968) records 2 braconids, one from each of the flowers of *S. longipes* and *Potentilla* sp.

IV.29.2.1.1. Apanteles

One specimen, a female was collected from the anthers of *Dryas integrifolia* on 30.VI, its activity was not ascertained, it appeared to be merely resting.

IV.29.2.2. Ichneumonidae

Oliver (1963) lists 19 genera of Ichneumonidae from Hazen Camp. Not all were collected on flowers. Imms (1964: 702) mentions that ichneumonids are "partial to flowers" and Müller (1873: 464-465) lists 13 forms for 43 flower visits.

IV.29.2.2.1. Atractodes

Oliver (1963) lists this genus with 6 undetermined species. On 20.VII.1967 I collected 2 males and 1 female from *Stellaria longipes* around Gilman Camp. One male was resting on a petal with its head directed away from the center of the flower in which there was also a specimen of *Stenomacrus* sp. The other two specimens were apparently imbibing nectar as in the chalcids. The female carried a little pollen, but had consumed none. One other male was collected at Gilman Camp on 21.VII on *S. longipes* as it rested.





IV.29.2.2.2. *Cryptus arcticus* Schiødtte

One female was collected on 10.VI.1967 at Hazen Camp from a male *Salix arctica* catkin; it carried no pollen, and its activity was not ascertained. Hocking (1968) records these insects from staminate catkins of *S. arctica*, *S. longipes*, *Braya* sp. and *Saxifraga* sp. These specimens were not collected on the flowers mentioned, the records are inferred from analysis of the pollen grains adhering to their bodies.

IV.29.2.2.3. *Hyposeter luctus* Davis

Hocking (1968) recorded 2 males from staminate catkins of *S. arctica* and *Braya* sp. from evidence of pollen adhering to them. I collected none from flowers in 1967.

IV.29.2.2.4. *Mesoleius* sp.

There are at least 5 species of *Mesoleius* at Hazen Camp (cf. Oliver, 1963). I collected 2 males (17.VII), 1 the prey of *Xysticus deichmanni* was already dead at the base of the filaments of a petal of *Dryas integrifolia*, the other was collected from *D. integrifolia* as it rested, behind Mt. McGill at about 650 m. Neither specimen carried pollen.

IV.29.2.2.5. *Mesoleptus* sp.

This genus is not listed by Oliver (1963).

One male was collected at Gilman Camp on 13.VII.1967 from the disc florets of *Arnica alpina*. Its abdomen was all that was visible as the insect was inverted presumably to reach the nectar. One female was collected at Gilman Camp on 20.VII on *S. longipes* as it



fed on the nectar; it stood on the sepals and petals and applied its mouthparts to the nectar.

IV.29.2.2.6. *Oresbius* sp.

This genus is not listed by Oliver (1963).

One specimen was collected from a staminate catkin of *Salix arctica*, it carried pollen but its activity was not ascertained.

IV.29.2.2.7. *Saotis* sp.

At least 1 species of *Saotis* is known from Hazen Camp (cf. Oliver, 1963). Two females were collected on 17.VII.1967 from the flowers of *D. integrifolia*. One had its head well down between the pistils and the filaments of an anthesed flower as it moved around presumably imbibing nectar. The other appeared to be resting, its head amidst the anthers. These insects had pollen on them.

IV.29.2.2.8. *Stenomacrus* sp.

There are at least 4 species of *Stenomacrus* at Hazen Camp (cf. Oliver, 1963). On 8.VII.1967 at Hazen Camp, 1 male and 1 unsexed specimen were collected from *Saxifraga Hirculus*. The male was resting on a petal while the other, in a different flower was actively running about the base of the corolla accompanied by a chalcid (see above); neither specimen carried pollen. On the same day another unsexed specimen was taken from *Dryas integrifolia*, and it was dusted with pollen grains. On 17.VII, 1 male was taken on *D. integrifolia* as it rested on a petal. Between 18.VII and 31.VII, 15 females and 4 males were collected from *Stellaria longipes* flowers at both Hazen Camp and around Gilman Camp. Three males were collected around



Gilman Camp on 20.VII, 2 had their mouthparts inserted into the nectar while they gripped the petals or sepals with their tarsi, the other was resting, its head directed away from the center of the flower in which there was also a female specimen of this species (see above). The remaining male was collected at Hazen Camp on 31.VII as it rested, it had one or two pollen grains on its right metacoxae. The first confirmed female was collected at Gilman Camp on 18.VII from *S. longipes* as it fed, its head down and its mouthparts into the nectar. On 20.VII, at Gilman Camp, 6 females were collected on *S. longipes*, 5 exactly as above, the other rested on the petals, its head directed away from the center of the flower, as is described for the male resting in the same flower (see above). Two females were noted as carrying pollen grains. The next day 4 females were collected from *S. longipes* at Gilman Camp, 1 carried pollen on its notum. At Hazen Camp, 1 female was collected as it rested on *S. longipes* on 26.VII; and 2 further were collected on *S. longipes* on 31.VII, 1 was imbibing nectar, and the other, dusted with pollen, was resting.

#### IV.29.2.2.9. Ichneumonidae (Unidentified)

Two specimens were observed but evaded capture. One was observed on *D. integrifolia* on 12.VII at Hazen Camp, and the other on *Arnica alpina* on 15.VII at Gilman Camp. Both specimens were large, having an estimated length of 15 mm.

Oliver (1963) lists the following genera and species which I have not recorded in flowers: *Bathythrix* sp., *Diplazon* sp., *Exochus pullatus* Tow., *Gelis* sp., *Himerta* sp., *Horogenes* sp., *Ichneumon lariae* Curtis, *Mesochorus* sp., *Opidnus* sp., *Orthocentrus* sp., *Phygadeuon*





3 spp., *Plectiscus* sp., and *Prolietus* sp.

It is likely that these could be found feeding on the nectar of flowers should an observer be in the right place at the right time.

#### IV.29.2.3. Microhymenoptera

One specimen was seen on a staminate catkin of *Salix arctica* on 3.VI.1967. Its activity was not ascertained. The specimen escaped.

#### IV.30      Bombidae

Two species of *Bombus* occur at Hazen Camp. Richards (1970) has discussed their nesting biologies and their zoogeographical affinities. Milliron and Oliver (1966) have written briefly on the usurpation of *B. polaris* Curt. nests by *B. hyperboreus* Schönh. at Hazen Camp. The rôles of arctic bumblebees as pollinators have recently been discussed by Chernov (1966) and Shamurin (1966). Richards (1970) summarizes much of the literature on flower visiting by arctic bumblebees.

I have made little attempt to separate the species. It is safe to say that most, probably over 90%, refer to *B. polaris* as Richards (1970) recorded only 16 (7.6%) of 210 bumblebees in 1967 and only 16 (6.4%) of 251 in 1968 visiting flowers as *B. hyperboreus*, all others were *B. polaris*. Furthermore, *B. hyperboreus* very rarely, if ever, produces workers.

The occurrence of bumblebees on flowers reflects the stage of development and requirements of the hives. At Hazen Camp the emergence of the overwintered *B. polaris* queens is almost synchronous and the subsequent colony development proceeds with a high degree of synchrony although as the season progresses some of this synchrony is lost.

The development of bumblebee colonies can be divided into 5



stages (see Free and Butler, 1959; Richards, 1970). Stage 1 is the emergence of the overwintered impregnated queens which then spend time feeding on nectar and pollen (Free and Butler, 1959: 6). Stage 2 consists of queens searching for suitable nest sites, and although the bees are frequently seen they do not visit many flowers (*op. cit.*, p. 6). During stage 3 the queens busy themselves establishing and building nests, and producing the first brood; they visit flowers, eating pollen for maturation of their ovaries and to feed the brood (*op. cit.*, pp. 8-9). At stage 4 the first workers emerge and gather nectar and pollen to feed both sexual and asexual larvae. The final stage 5 comes with the emergence of the new sexuals and the decline of the colony; pollen is no longer needed and the remaining bees feed on nectar (*op. cit.*, pp. 32-34). Table 7 shows the occurrence of bumblebees on flowers through stages 1 to 5 in 1966, 1967, 1968, and partially in 1963. Unfortunately Richards' (1970) data on flower visiting bees, although based on more observations, is too vague to allow any accurate resolution in terms of nest stages.

In 1966 and 1967 all queens seen on flowers during stage 1 were visiting *Saxifraga oppositifolia* (in 1966: 2, 14.VI; 13, 16.VI; 20, 18.VI; 1, 19.VI; in 1967: 4, 30.V; 5, 31.V; 2, 2.VI; 1, 4.VI), while in 1968 both male and female catkins of *Salix arctica* were also visited (on *S. oppositifolia* 2, 15.VI; 3, 16.VI; on male *S. arctica* 4, 16.VI; 1, 17.VI; on female *S. arctica* 1, 17.VI). No queens had collected pollen in their corbiculae. They fed extensively on nectar. When visiting *S. oppositifolia* they flew below 15 cm directly from flower to flower. They landed on the petals which they gripped with all 6 tarsi and lowered their heads to project their proboscides







Table 7.

The occurrence of bumblebees on flowers through nest development duration of each.

Stage	1963*	Duration			Number on Flowers			
		1966	1967	1968	1963	1966	1967	1968
1	--	14.VI	27.V	14.VI	--	36	12	26
		to 19.VI	to 5.VI	to 17.VI			(69)	(59)
2	--	20.VI	6.VI	18.VI	--	1 <sup>†</sup>		0 <sup>∇</sup>
		to 29.VI	to	to 24.VI			2	
3	21.VI	30.VI	27.VI	25.VI	2	0		3
	to 3.VII <sup>Δ</sup>	to 5.VII		to 4.VII				
4	3.VII	6.VII	28.VI	5.VII	82+	30+	29	6
	to 29.VII <sup>✓</sup>	to 1.VIII	to 31.VII	to 13.VII <sup>Φ</sup>			(109)	(134)
5	--	30.VII	13.VII	22.VII	--	18	24	35
		to 2.VIII	to 1.VIII	to 3.VIII				

\* Data from Hocking (1968)

† 34 seen nest hunting in this period

∇ 24 seen nest hunting on 19.VI (Richards, 1970)

Δ Duration probably incomplete before this date

✓ Duration probably incomplete after this date

Φ Data incomplete, not in camp.

Numbers in brackets extrapolated from Richards (1970) (those in stage

stages 1 to 5 in 1966, 1967, 1968, and partially 1963 and the approximate

Number with Pollen Load				Number Nectar Feeding			
1963	1966	1967	1968	1963	1966	1967	1968
--	0	0	1	--	36	12	26
--	0		0	--	1		0
		2				--	
0	0		3	--	0		--
29	12	7	--	34+	11+	24+	--
--	0	0	0	--	15+	22+	35

1 represent continuation through to stage 3).



to imbibe nectar. On two occasions I observed bees closely enough to watch them lower their antennae before feeding. When on catkins they fed first from the lower florets, then spiralled upwards feeding rapidly as they went. Free and Butler (1959) state that the newly emerged queens feed on pollen, presumably to mature their ova. None were observed feeding on pollen at Hazen Camp; but on 16.VI.1968 one was watched chewing the anthers of *Salix arctica* and may have been feeding on pollen. Pollen feeding on *S. oppositifolia* may well have been missed as its detection requires closer observation than nectar feeding.

During stages 2 and 3 the queens spend most of their time in activities other than visiting flowers. During stage 2 they are searching out suitable nest sites. In 1966 between 21.VI and 29.VI over 30 queens were watched investigating lemming holes, but only 1 took a quick sip from a *S. oppositifolia* flower; *S. oppositifolia*, *Dryas integrifolia*, *Cassiope tetragona*, *Salix arctica*, *Lesquerella arctica*, and *Draba* spp. were blooming all around. Similarly Richards (1970) records 24 queens nest-hunting on 19.VI.1968. During stage 3 the queens have established their nests and spend much of their time inside, incubating eggs and brood. The queens make short sorties for nectar and pollen (Richards, 1970) reports 20 sorties of about 30 minutes each in a 24-hour period for one nest) to feed the brood and themselves. Thus queens are not as commonly seen on flowers at this time as previously. This is accentuated by the probable mortality of queens unsuccessful in establishing nests, and by the great increase in availability of flowers. Thus in 1967 between 6.VI and 27.VI only 2 queens were seen, and between 18.VI and 2.VII.1968 only 3. All 5



carried pollen loads. . . On 25.VI.1968, one queen was watched gathering pollen from *Salix arctica*; it visited 8 catkins. On 26.VI.1968, another was watched as she visited catkins of *S. arctica*; 5 staminate, 4 pistillate, and 2 staminate, primarily for nectar as she already had full corbiculae. On 30.VI.1968 one was watched as she collected pollen from 3 staminate catkins. . . On 9.VI.1967 both queens were visiting *Saxifraga oppositifolia*.

It is not until stage 4 when the first brood emerges that bumblebees become frequent on flowers. The workers, primarily, and the queens visit flowers for nectar and pollen for the remaining worker brood as well as the developing sexual larvae. During this time the bees visit a diverse array of available flowers. The results of observations in 1966, 1967, and 1968 are presented in Table 8.

During stage 5 no pollen is needed as there is no developing brood. Bees visiting flowers take only nectar. The workers seem to die soon after the sexuals emerge; I saw only two after 30.VII.1966 against more than 16 sexuals between then and 2.VIII.1966. Flower visits are given in Table 9.





Table 8.

Bumblebees of different castes on different flowers and the purpose of their visits throughout nest stage 4; Hazen and Gilman Camps, 1966-1968.

Explanation of Symbols

Castes:

Q -- queen  
W -- worker  
M -- male

Purposes:

N -- imbibing nectar  
P -- collecting pollen  
N+P -- imbibing nectar while carrying a  
pollen load  
U -- unknown (activity or caste)

Δ      extraplated from Richards (1970)  
▽      some observations may belong in stage 5  
#      other observations included in stage 1  
A, B, same individual on other species of flower



<u>Flower</u>	<u>Caste</u>	<u>Number</u>	<u>No. and purpose of visit</u>				<u>Dates</u>	<u>Comments</u>
<i>Salix arctica</i> (staminate catkins) #	W	1	-	-	--	1	9.VII.1967	Visited 1 catkin
	Q	1	-	1	--	-	30.VI. 1968	Visited 3 catkins
<i>Stellaria longipes</i> ∇	W	2,1	3	-	--	-	17*,18 <sup>+</sup> .VII.1966	*Visited 6 flowers +Gilman Camp
	U	1	1	-	--	-	28 <sup>B</sup> .VII.1966	Visited 50+ flowers
<i>Papaver radicatum</i>	U	1	-	1	--	-	18.VII.1966	Visited 18+ flowers, see also <i>D. integrifolia</i> Gilman Camp *appeared to try to feed on nectar
	W	1	-	1	--	--	18.VII.1966	
	W	1,2	-	1	--	2*	13.VII.1967	
	W	2 Δ					1967	
	M	1 Δ					1967	
<i>Potentilla nivea</i>	W	1	-	-	1	-	14.VII.1967	Gilman Camp Visited 10+ flowers
	W	1	-	-	1	-	30.VII.1967	
<i>Dryas integrifolia</i>	U	1,1	-	-	--	2	10,11.VII.1966	Visited several, visited 3 flowers
	Q	1	-	-	--	1	18.VII.1966	Visited 100+ flowers, see also <i>P. radicatum</i> Visited 2 flowers, see also <i>P. arctica</i> Both visited 20+ flowers
	W	1	1	-	1	-	18.VII.1966	
	W	1	1	-	1*	-	5.VII.1967	
	W	2	2	-	--	-	9.VII.1967	



<u>Flower</u> <i>Dryas</i> <i>integrifolia</i>	<u>Caste</u>	<u>Number</u>	No. and purpose of visit				<u>Dates</u>	<u>Comments</u>
			<u>N</u>	<u>P</u>	<u>N+P</u>	<u>U</u>		
	W	2,5,1	8	-	-	-	10, 13, 31.VII	Visited 2 flowers
	W	1	1	-	-	-	11.VII	Visited 1 flower
	W	1	-	-	-	1	16.VII	
	W	1	-	-	-	-	11.VII.1968	Visited 3 flowers
	W	1	-	-	-	-	6.VII.1968	Visited 2 flowers, see
	W	1	1	1	1	1	6.VII.1968	also <i>P. capitata</i> and
								<i>P. arctica</i>
	Q	4					ca. 16.VI-3.VIII.	<i>B. polaris</i>
	W	44					1967VΔ	
	M	1						<i>B. hyperboreus</i>
	Q	1						
	M	1						<i>B. polaris</i>
	Q	4					ca. 1.VII-22.VII.	
							1968VΔ	
	W	16						<i>B. hyperboreus</i>
	Q	5						
							ca. 28.VI-26.VII.	<i>B. polaris</i>
	W	10					1967	
	W	13					ca. 2.VII-25.VII.	<i>B. polaris</i>
	M	3					1968	
	U	1,1,2,2,1	-	-	-	-	6,7,11,13,15.VII.1966	
	U	1,1	0	2	0	0	7,8.VII.1966	
	Q	1	-	-	-	1	10.VII.1966	
	W	1,1	-	-	-	2	10.30A.VII.1966	
	W	1	0	1	0	0	20.VII.1966	
	U	1	0	0	1	0	15.VII.1966	
	W	1	-	-	-	1	28.VI.1967	
	W	1	1	0	0	0	12.VII.1967	
	W	1,2	0	0	3	0	5,*12.VII.1967	
<i>Cassiope</i> <i>tetragona</i> VΔ								*Visited 4 plants, many
								flowers, see also
								<i>D. integrifolia</i>
<i>Pedicularis</i> <i>arctica</i>								
								A - see <i>P. capitata</i>





Flower	Caste	Number	No. and purpose of visit				Dates	Comments
			N	P	N+P	U		
<i>Pedicularis arctica</i>	W	2	2	0	0	0	*2, 4.VII.1967	*Visited 16 plants, many flowers
	W	2, 1	0	0	2	1	11.VII.1968	<i>B. hyperboreus</i>
	Q	1	1	0	0	0	13.VII.1968	See also <i>P. capitata</i>
	W	1	0	1	0	0	6.VII.1968	and <i>D. integrifolia</i>
	Q	30 Δ					ca. 25.VI-27.VII. 1967	<i>B. polaris</i>
	W	9 Δ						<i>B. hyperboreus</i>
	Q	5 Δ						<i>B. polaris</i>
	Q	23 Δ					ca. 1.VII-29.VII. 1968	
	W	15 Δ						<i>B. hyperboreus</i>
	Q	3 Δ						
<i>Pedicularis capitata</i>	W, Q, U	1, 1, 1	-	-	--	3	30 <sup>A</sup> , 21, 13*.VII.1966	*Visited 10-15 flowers Asee <i>P. arctica</i>
	W	2	0	1	1	0	11.VII.1968	See also <i>P. arctica</i>
	W	1	1	-	--	-	6.VII.1968	and <i>D. integrifolia</i>
	Q	5 Δ					ca. 27.VI-22.VII. 1967	<i>B. polaris</i>
	W	5 Δ						<i>B. polaris</i>
	Q	4 Δ						<i>B. hyperboreus</i>
	Q	19 Δ					ca. 5.VII-22.VII. 1967	<i>B. polaris</i>
	Q	19 Δ						<i>B. polaris</i>
	Q	2 Δ						<i>B. hyperboreus</i>



<u>Flower</u>	<u>Caste</u>	<u>Number</u>	<u>No. and purpose of visit</u>				<u>Dates</u>	<u>Comments</u>
<u>Flower</u>	<u>Caste</u>	<u>Number</u>	<u>N</u>	<u>P</u>	<u>N+P</u>	<u>U</u>	<u>Dates</u>	<u>Comments</u>
<i>Arnica alpina</i>		W4, U2	-	-	4	2	1.VII.1966	
	U	1,2	-	-	--	3	14,18.VII.1967	Gilman Camp
	W	1	-	-	--	1	14.VII.1967	Visited 3 inflores-
			-	-				cences, Gilman Camp
	W	1	-	-	1	--	17.VII.1967	Gilman Camp
	W	1	1	-	--	-	31.VII.1967	Gilman Camp
	W	1ΔV 1ΔV					1967 1968	Gilman Camp
<i>Taraxacum arctogenum</i> ∇	W	1	1	-	--	-	28 <sup>B</sup> .VII.1966	Visited 2 inflorescences



Table 9.

Bumblebees of different castes on different flowers during nest stage 5; Hazen, Gilman, and Tanquary Fiord Camps, 1966-1968.

<u>Flower</u>	<u>Caste</u>	<u>Number</u>	<u>Date</u>	<u>Comments</u>
<i>Salix</i> <i>arctica</i>	M	1	31.VII.1967	imbibing nectar
	M	1	28.VII.1966	on seed head, see <i>S. longipes</i> <sup>1</sup>
	M	1	26.VII.1967	on seed head <sup>1</sup>
<i>S. longipes</i>	M	1	28.VII.1966	visited 50+ flowers and developed <i>Salix arctica</i> seed head <sup>1</sup>
	M	1	30.VII.1967	visited 6+ flowers, imbibing nectar
<i>C. alpinum</i> & <i>Stellaria</i> <i>longipes</i>	S	20+	3.VIII.1968	all visited several flowers (3 to many) imbibing nectar, some males crawling from flower to flower. Actively avoided <i>Erigeron compositus</i> , <i>Saxifraga cernua</i> , <i>S. caespitosa</i> , <i>S. flagellaris</i> , <i>Papaver radicatum</i> which were more abundant in places. Behind Mt. McGill, in stream bed 500-900 m
<i>Cerastium</i> <i>alpinum</i> & <i>Dryas</i> <i>integrifolia</i>	M	1	1.VIII.1967	visited several flowers of each. Mt. Omingmak, ca. 800 m
<i>D. integrifolia</i>	M	1	13.VII.1967	imbibing nectar





<u>Flower</u>	<u>Caste</u>	<u>Number</u>	<u>Date</u>	<u>Comments</u>
<i>Epilobium latifolium</i>	M	1,1,1	22, 27, 28.VII. 1968	all visited between 3 and 16 flowers imbibing nectar. Tanquary Fiord
<i>Pedicularis arctica</i>	W	1	30.VII.1966	see Table (stage 4)
	Q	1	30.VII.1966	
<i>P. capitata</i>	W	1	30.VII.1966	see Table (stage 4)
<i>Arnica alpina</i>	M?	8	1.VIII.1966	Gilman Camp
	M?, U	6,2	2.VIII.1966	Gilman Camp
	S	19	13.VII-20.VII. 1967	two observed imbibing nectar, 3 dusted with pollen on venter. Gilman camp



PART V

FLORAL ATTRACTANTS FOR INSECTS

V.1. Introduction

Insects are not necessarily attracted to flowers by colour or odour alone. Flowers attract insects in many ways, from overt advertising to subtly presenting combinations of characters which the insects concerned can associate with rewards.

I have therefore divided the attractants of flowers into two modes. Firstly, primary attraction, possibly brought about by innate responses in insects drawing them to the flowers; into this category fall colour, brightness (saturation), size, outline length, movement, and smell. Secondly are attractants which possibly rely on the previous experience of the insects; into this category fall combinations of the above, signifying ease of attaining rewards, and the presence of incidental benefits which can be associated with rewards. One floral attractant may fall into either mode, according to the insect in question: it is form numeral. Rewards come as food, nectar or pollen or prey or any combination thereof; comfort, as in warmth; protection from weather or predators; or a mate. I do not intend to suggest in this paragraph that in order to attain a reward, an insect must first learn that it is there. Insects vary widely in their ability to learn, and different species have instincts in relation to their biologies and physiological states.



V.2. Corolla Colours and Insect Spectral Sensitivity at Hazen Camp

V.2.1. Aims

The aims of the following study were to spectrally analyse the colours of arctic flowers, and their associated vegetative parts, and some background materials. This was done in conjunction with a study into the gross colour discrimination of some arctic insects, and is, in part, aimed at demonstrating the relationship between flower colours and insect colour discrimination.

V.2.2. Flower Colours: Review

Plateau (1899, 1900a,b) and others did work on the colours of flowers in relation to insect vision. The first detailed investigation into the physical nature of flower colour was done by Exner and Exner (1910). At this early stage nothing was known about ultraviolet reflection by flowers, although as early as 1872 Kraus had found ultraviolet reflection from some petal extracts. In 1923, Richtmyer using a small quartz spectrograph found ultraviolet reflection from flowers. Lutz (1924, 1933) photographed ultraviolet reflections from flowers using a pin hole camera; and his method, with improvements such as a quartz lens and built in grey scale, was used by Daumer (1958) and Mazokhin-Porshnyakov (1959) to do extensive analyses of flower colours. Mosquin (1969, pers. comm.) and Eisner *et al.* (1969, and Eisner, pers. comm.) are currently involved in similar studies.

Even so, floral colours are often studied today in relation to human spectral sensitivity and are difficult to interpret in reference to insect colour vision. Weevers (1952) has reviewed the subject from biochemical and phytogeographical standpoint. Green pigments are





chlorophylls (primarily A and B), yellow pigments are carotenes and xanthophylls, red and blue pigments are anthocyanins, and white pigments are anthoxanthin compounds which absorb ultraviolet strongly. As Weevers (1952) points out there are many complicating factors which may alter the effects of the pigments. Weevers (1952) discredits the theory of phytogeographical differences in the frequency with which different colours occur in flowers, although he admits that alpine floras tend to have more blue and violet flowers than others. He does not mention the arctic floras. Tikhomirov (1959) and Shamurin (1966b) have considered this problem and Tikhomirov (1959) remarks on the old observation of the preponderance of yellow and white flowers. Both Weevers' (1952) and Tikhomirov's (1959) data are tabulated in the results (Table 11).

### V.2.3. Flower Colours of the Hazen Flora

#### V.2.3.1. Materials and methods

The colours of many of the arctic flowers occurring at Hazen Camp area were examined photographically using a series of wide band monochromatic filters (Table 10). Extension bellows with an Asahi Pentax Quartz Takumar 1: 3.5/85 mm lens were used on a 35 mm reflex camera. The filters were mounted onto the front of the apparatus so that they were easily interchangeable. The film used was Kodak Tri-X panchromatic (ASA 400) as it is fast, and has almost uniform sensitivity over the range of insect and human visions (Kodak publication no. p-9, 1967; Fig. 5). The film was developed in Kodak D-76 at Hazen Camp.

The filters are not all of equal density, the spectral distribution of solar energy is not uniform, and the film is not exactly equally



sensitive in all wavelengths. These variables were all compensated for in one step. A small pellet of magnesium oxide, which reflects almost equally in all wavelengths of light (Weast, 1969), was placed on black flock paper, which absorbs almost all the visible light, and photographed in direct sunlight through each filter over a wide range of exposures. The developed film was examined and a comparison of the various exposures revealed the point of maximum contrast between the magnesium oxide and the black flock paper. This point of maximum contrast was taken as the correct exposure for the filter under consideration; for at this point as much light as possible was being reflected from the magnesium oxide, and as little as possible from the black flock paper. This correct exposure was recorded from each filter as a multiple of the exposure value obtained from a reflected light exposure meter (Sekonic) held 6 cm from the object.

Small paper labels were used in the flower photographs to mark which filter was being used. The reflectance of these labels was measured relative to a block of  $\text{MgCO}_3$  using a Cary Model 14 spectrophotometer from 350-400 nm. The samples were illuminated diffusely with light from a hydrogen lamp via an integrating sphere and passed through a monochromator with a bandwidth of about 6 m $\mu$  and directed approximately normal to the samples (A. R. Robertson, Radiation Optics, National Research Council, Ottawa; in pers. comm. to Dr. T. Mosquin). The paper was found to reflect more or less equally in all wavebands except ultraviolet, with a reflectance of about 85%, when compared photographically with magnesium oxide (see also Weast, 1969).

Further difficulty arose when I attempted to focus the short wavelengths transmitted by filters 18A, 35, and 48. These wavelengths







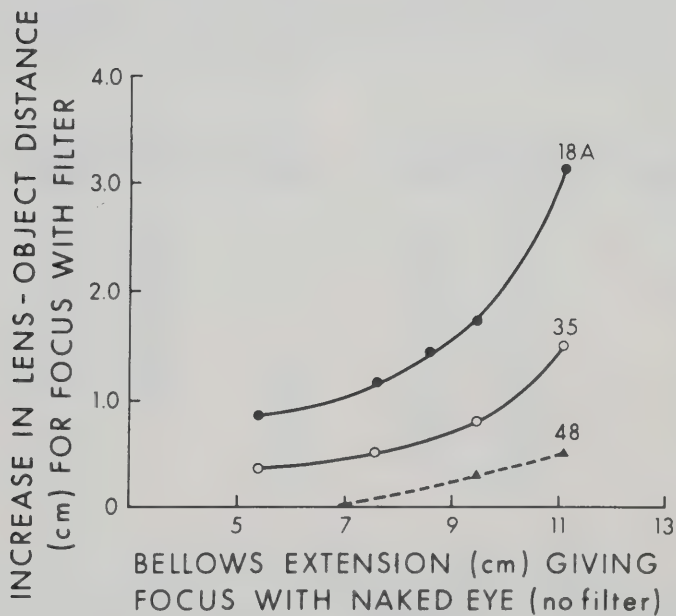
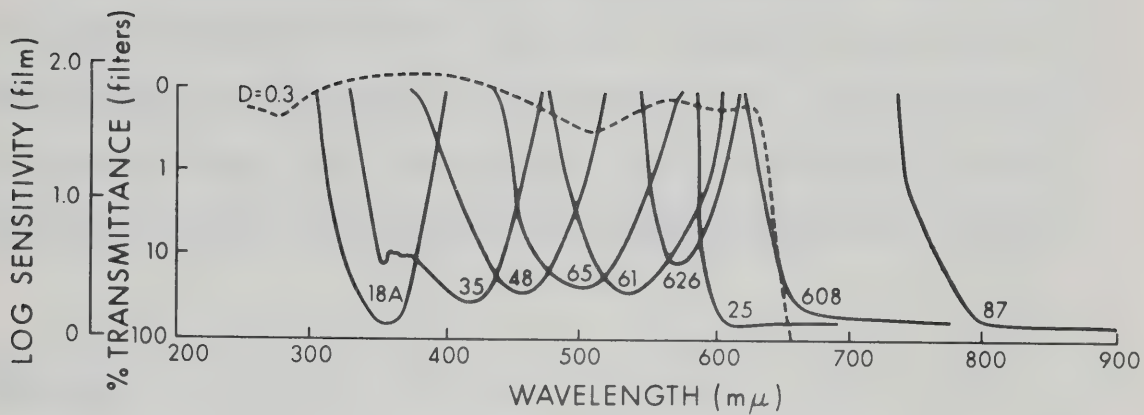
Figure 5.

Per cent transmissivity of the filters used for analysis of corolla colour and spectral discrimination experiments on insects (data from Kodak publication B-3 (1966) and Ilford Technical Information Sheet F 20-1); and film sensitivity (log reciprocal of exposure in ergs/cm<sup>2</sup> required to produce specific density above density of base plus fog,  $D = 0.3$ ) of Kodak Tri-X pan film (Technical sheet 24-320 supplied from Kodak on request); according to wavelength in millimicrons.

Figure 6.

Focus adjustment for filters 18A, 35, and 48 (for filters 35 and 48 the curves are not accurate, but served adequately).

To use: Focus on object through the camera lens on bellows. Measure extension of bellows. Place filter in front of lens. Increase lens-object distance by decreasing the bellows extension.





do not focus at the same lens distance as the longer wavelengths in our visible spectrum. The lens-film distance had to be shortened considerably, and by experiment Fig. 6 was prepared.

Fresh flowers and other materials were mounted with insect pins on a board covered with black flock paper. Using the above filter factors and focus adjustments, the photographs were taken immediately to prevent wilting. They were analysed in much the same way as was used by Lutz (1924), Daumer (1958), and Masokhin-Porshnyakov (1959).

Table 10.

The filters: their transmission ranges, filter factors in multiples of light meter reading at 6 cm, per cent reflectance of paper labels with respect to magnesium oxide and magnesium carbonate for each filter, and reflectance value used for calculation of flower colour.

<u>Filters make &amp; number</u>	<u>Transmission range mm</u>	<u>Filter factor</u>	<u>Reflectance of paper (%)</u>	<u>Reflectance value used (%)**</u>
Kodak 18A	300 - 400	6	< 30 - 85	60
Kodak 35	350 - 450	2	45 - 90	85
Kodak 48	400 - 500	3	80 - 90	85
Kodak 65	450 - 550	6	80 - 90	85
Kodak 61	500 - 600	4	80 - 90	85
Ilford 626	550 - 650	8	80 - 90	85
Kodak 25	600 -	3	80 - 90	85
Ilford 608	650 -	48	80 - 90	85
Kodak 87	750 -	---	-*	--

\* Film loses sensitivity at about 650 mμ (Fig. 6).

\*\* Reflectance values used to calculate flower colours represent reflectance of paper at peak of transmission of the filters.

#### V.2.3.2. Results

The results are presented in Fig. 7 to 34 and Appendix I which give the reflectance of the flowers. A number of other flowers were tested







Figure 7.

Photographs showing reflectance of an inflorescence of *Erigeron compositus* according to the trichromatic colour schemes of insects (within solid line) and men (within broken line).

Upper right - ultraviolet, insect blue.

Lower right - blue, insect green.

Lower left - yellow (green), insect red.

Upper left - red, insect infrared.

Note: There is no ultraviolet reflected, no blue reflected from disc, yellow-green to red are reflected from whole inflorescence. Inflorescence is white with yellow center or insect-yellow with insect-red center.

Figure 8.

Spectral distribution of reflection from inflorescence of *Erigeron compositus*. Broken line, disc florets, solid line, ray florets, and whole inflorescence after convergence with broken line.

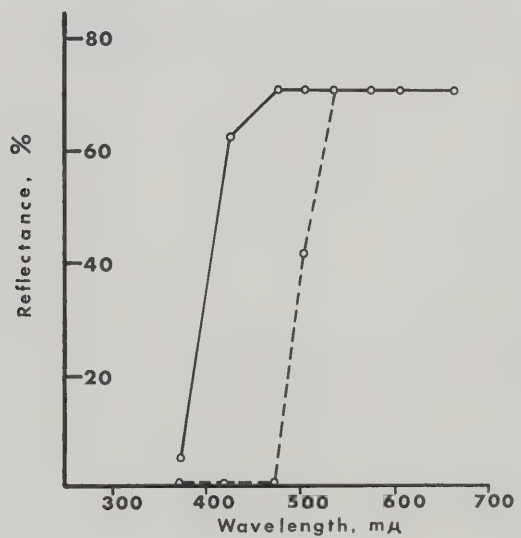
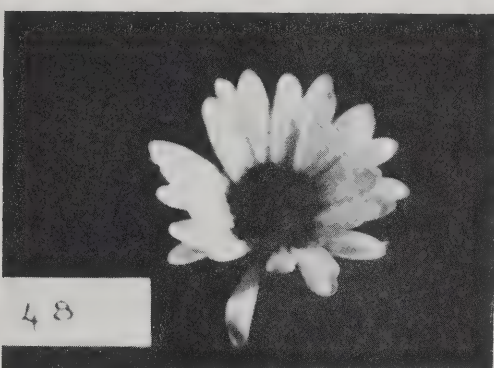
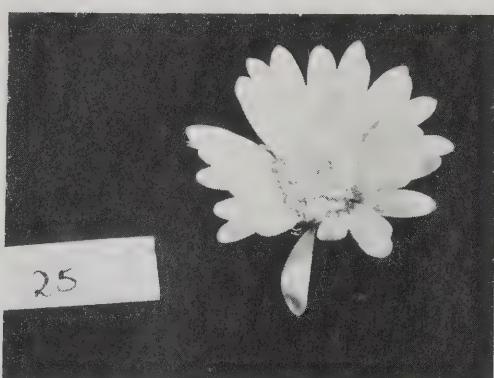
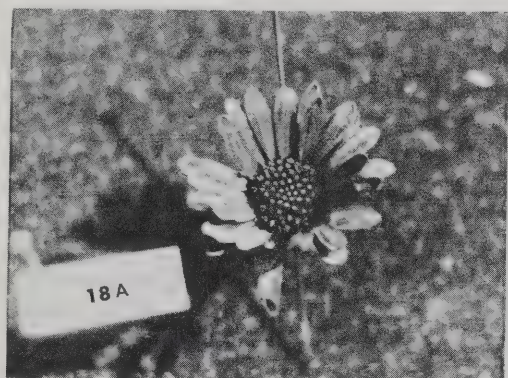






Figure 9.

Spectral distribution of reflection from an inflorescence of *Erigeron eriocephalus*. As Fig. 8 but solid line with solid circles, pubescence of involucre.

Figure 10.

Spectral distribution of reflection from an inflorescence of *Chrysanthemum integrifolium*. As in Fig. 8.

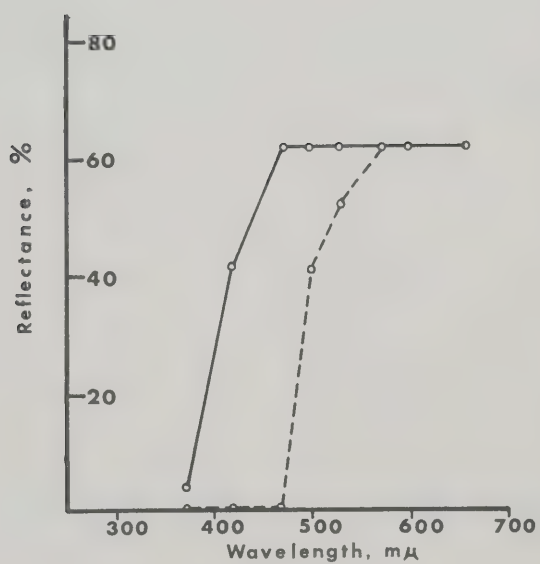
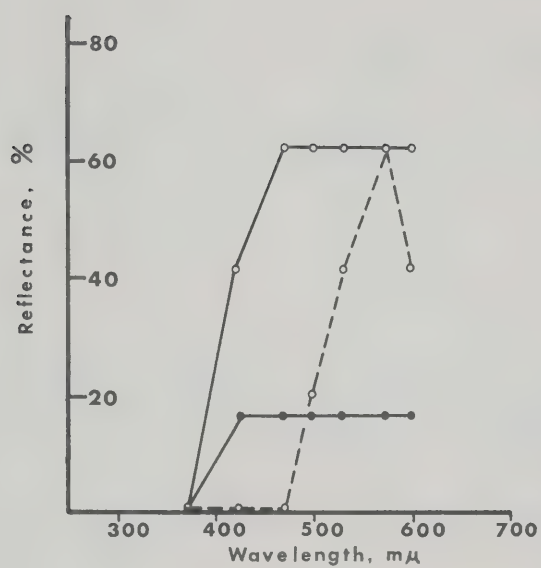








Figure 11 (upper left).

Spectral distribution of reflection from a flower of *Cerastium alpinum*.

Figure 12 (upper right).

Spectral distribution of reflection from an inflorescence of *Polygonum viviparum*.

Figure 13 (lower left).

Spectral distribution of reflection from some white flowers; open circles, *Stellaria longipes*; closed circles, *Braya humilis*, *Draba groenlandica*.

Figure 14 (lower right).

Spectral distribution of reflection from a flower of *Cassiope tetragona*.

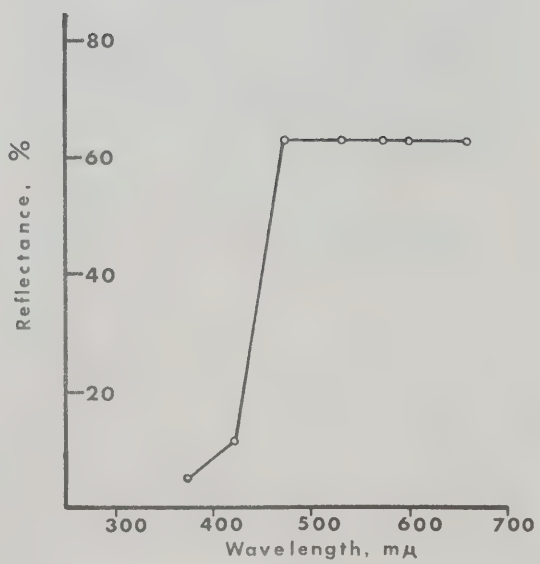
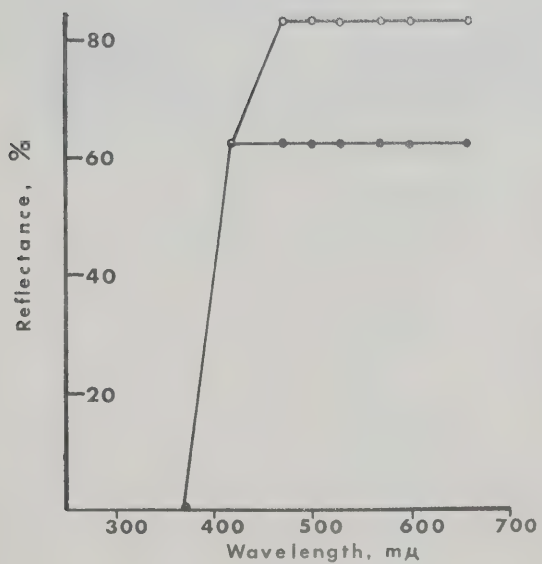
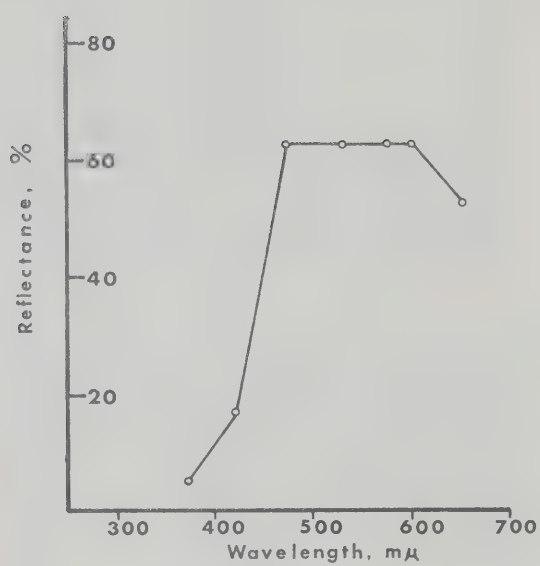
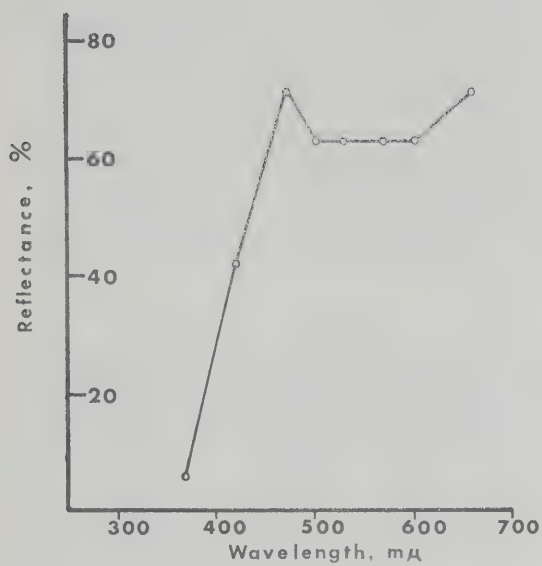








Figure 15.

Photographs showing reflectance of a flower of *Dryas integrifolia* according to the trichromatic colour scheme of insects (within solid line) and men (within broken line).

Upper right - ultraviolet, insect blue.

Lower right - blue, insect green.

Lower left - yellow (green), insect red.

Upper left - red, insect infrared.

Note: There is no ultraviolet reflection, no blue is reflected from the sporophylls, but some is reflected from the petals. Yellow-green to red is reflected by the whole flower. Flower is pale yellow with yellow center or insect-orange with insect-red center.

Figure 16.

Spectral distribution of reflection from a flower of *Dryas integrifolia*. Open circles, petals; closed circles, sporophylls.

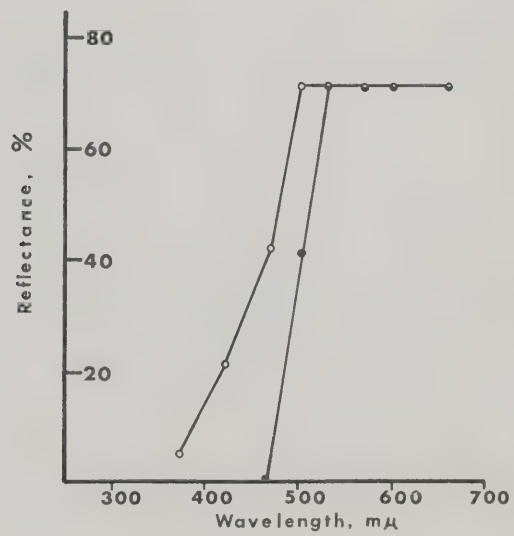






Figure 17.

Spectral distribution of reflectance from flower of  
*Papaver radicatum*. (Upper right)

Figure 18.

Spectral distribution of reflectance from flower of  
*Potentilla nivea*. (Upper left)

Figure 19.

Spectral distribution of reflectance from flowers of  
*Lesquerella arctica* and *Draba Bellii*. (Below)

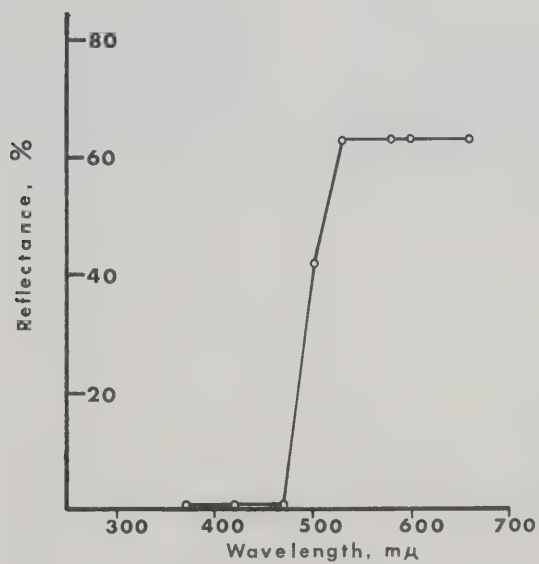
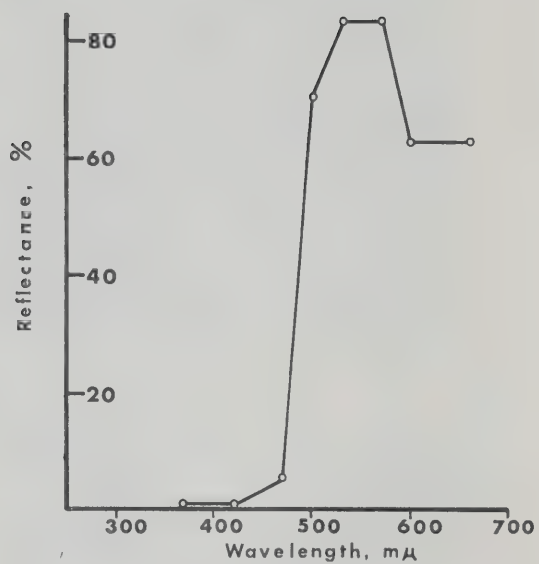
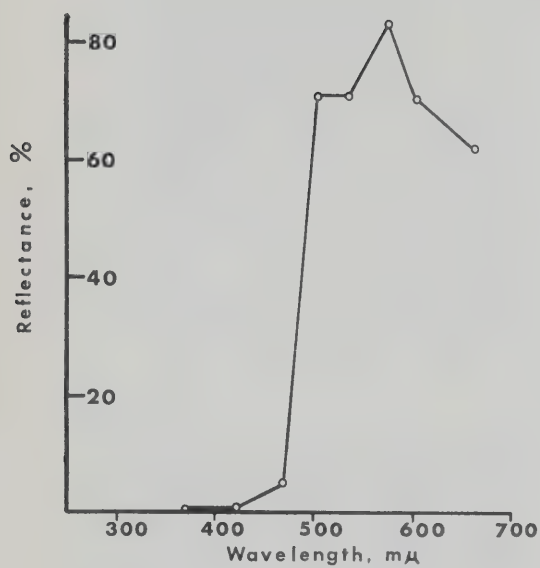








Figure 20.

Photographs showing reflection from an inflorescence of *Arnica alpina* according to the trichromatic colour schemes of insects (within solid line) and men (within broken line).

Upper right - ultraviolet, insect blue.

Lower right - blue, insect green.

Lower left - yellow (green), insect red.

Upper left - red, insect infrared.

Note: There is no ultraviolet reflection from the disc florets or from the proximal parts of the rays; there is no reflection in the blue. Inflorescence is yellow or insect red in the center and insect purple peripherally.

Figure 21.

Spectral distribution of reflection from an inflorescence of *Arnica alpina*. Broken line, distal portion of ray florets; solid line, entire inflorescence or center only before convergence with broken line.

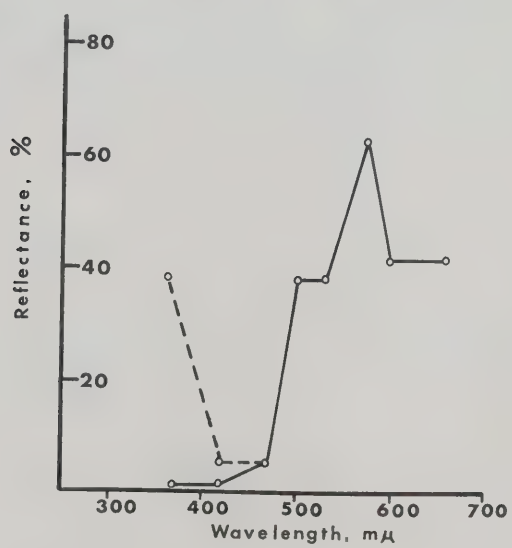






Figure 22 (upper right).

Spectral distribution of reflection from an inflorescence of *Taraxacum arctogenum*. As in Fig. 21.

Figure 23 (upper left).

Spectral distribution of reflection from a flower of *Ranunculus sulphureus*. Broken line, distal parts of petals; solid line entire petals, or proximal parts only before convergence with broken line.

Figure 24 (lower right).

Spectral distribution of reflection from a flower of *Pedicularis capitata*. Broken line, parts of helmet and lip, solid line entire flower or parts not reflecting according to broken line before convergence of the two lines.

Figure 25 (lower left).

Spectral distribution of reflection from a flower of *Saxifraga Hirculus*. Broken line distal parts of petals and basal swellings; solid line, entire petals except for orange spots in basal half of petal (dotted line) or basal half of petals only before convergence with broken line.

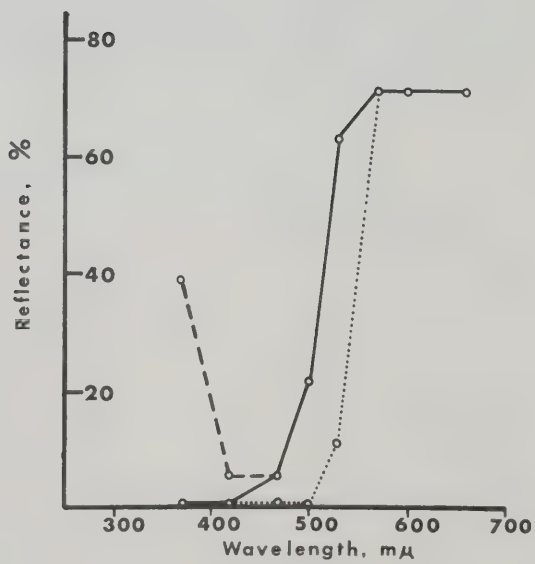
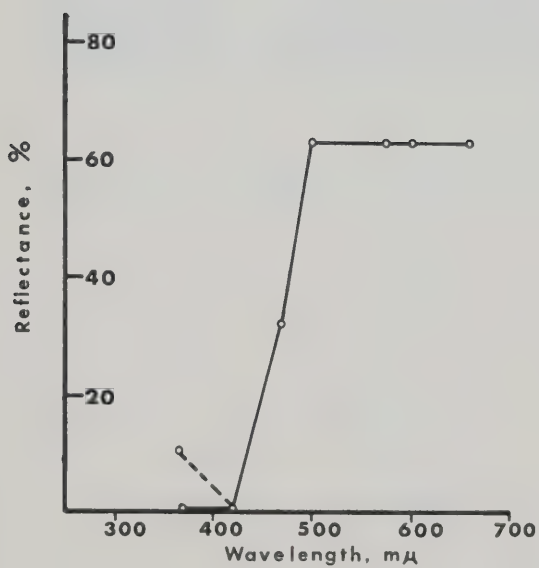
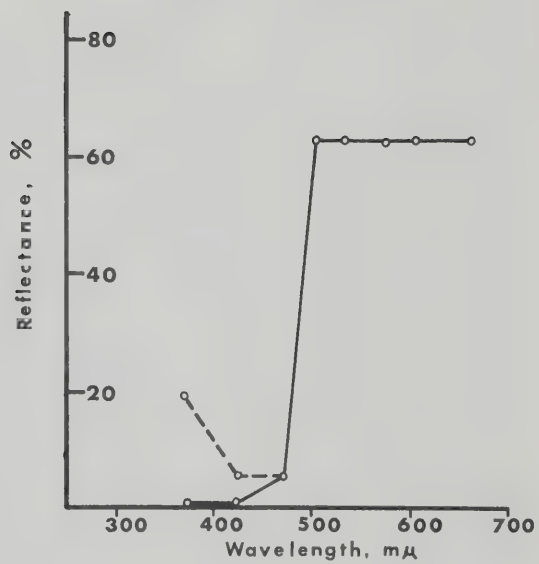
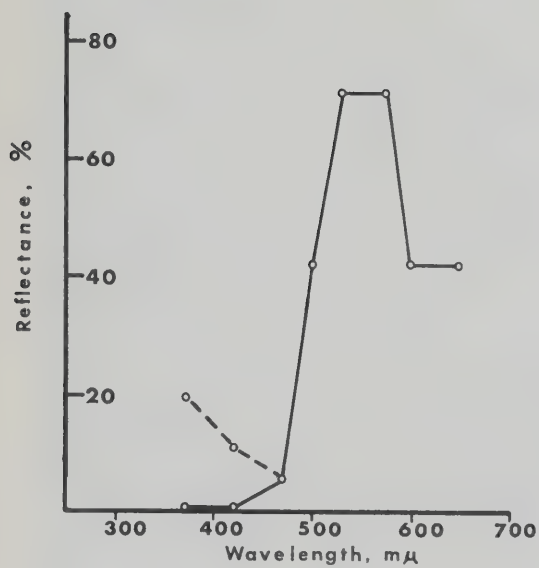








Figure 26.

Photograph showing ultraviolet reflection from *Cerastium alpinum* (left) (see also Fig. 11) and *Saxifraga Hirculus* (right) (see also Fig. 25).

Figure 27.

Spectral distribution of reflection from flower of *Saxifraga tricuspidata*. Dotted line, dark red spots, on petals; solid line, rest of petals.

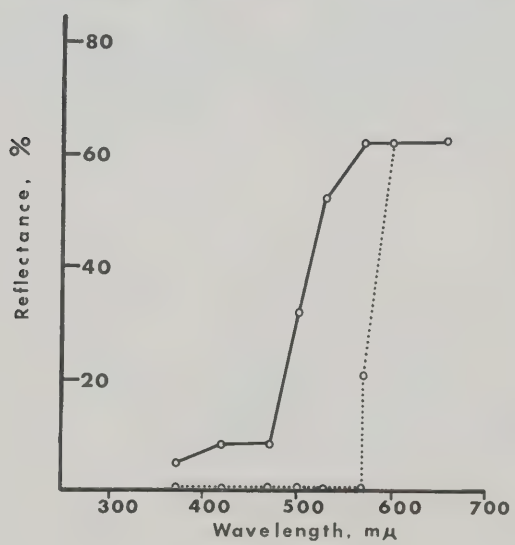
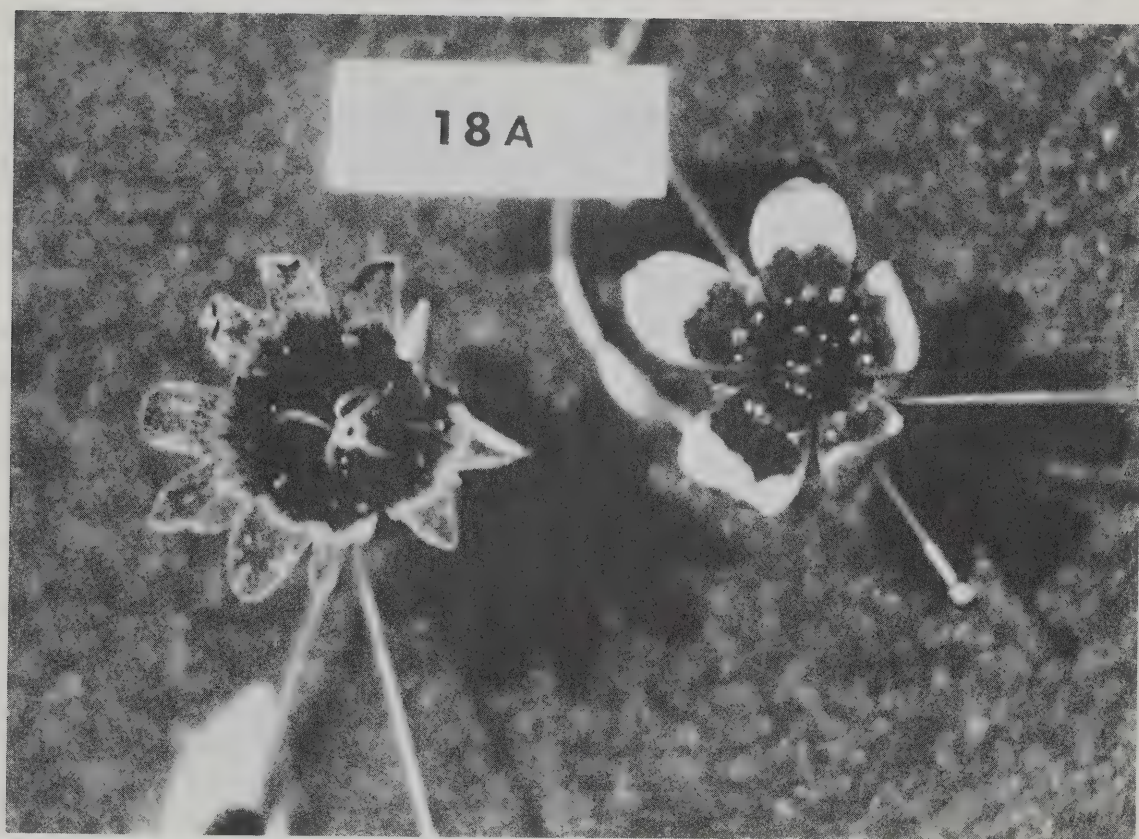






Figure 28.

Photographs showing reflection of staminate (right) and pistillate (left) catkins of *Salix arctica* in the ultraviolet (left) and red (right) wavebands.

Figure 29.

Spectral distribution of reflection from catkins of *Salix arctica* (see also Fig. 28).

Solid line, open circles; anthesed stamens, pollen.

Solid line, solid circles; receptive stigmas.

Dotted line, open circles; pubescence.



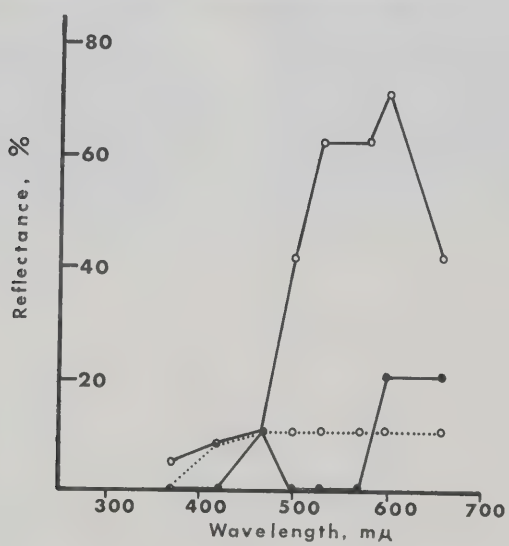






Figure 30.

Photographs showing reflection from a flower of *Epilobium latifolium* according to the trichromatic colour schemes of insects (with solid line) and men (within broken line).

Upper right - ultraviolet, insect blue.

Lower right - blue, insect green.

Lower left - yellow (green), insect red.

Upper left - red, insect infrared.

Note: There is some ultraviolet reflection; more blue, except on veins; little green to yellow; and strong reflection of red.

Inflorescence is purple or insect light green with dull green veins.

Figure 31.

Spectral distribution of reflection from a flower of *Epilobium latifolium*. Closed circles, veins on petals; open circles, rest of petals.

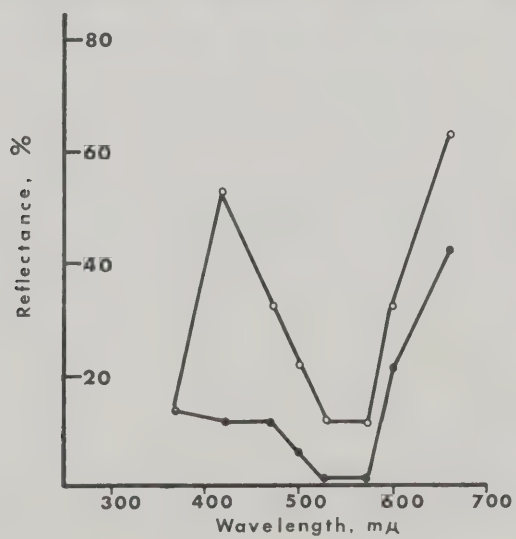
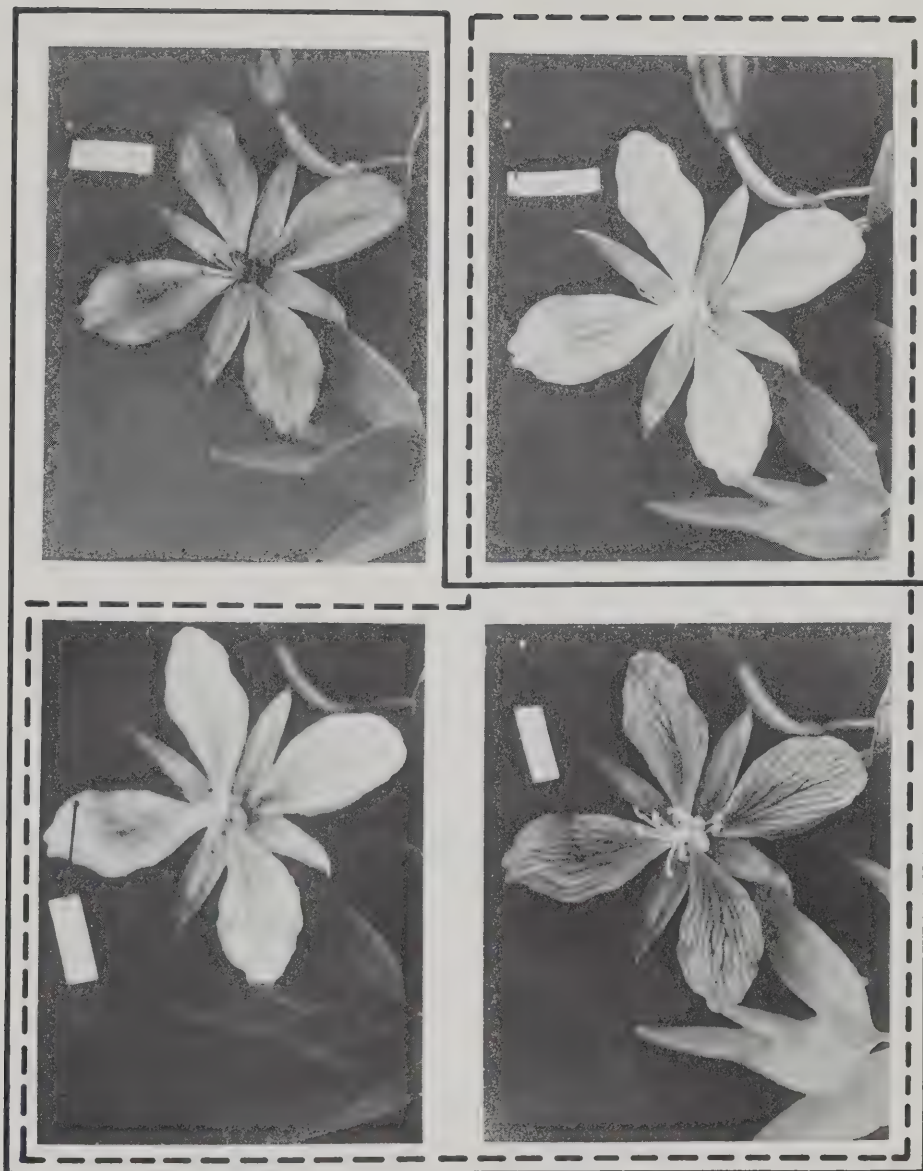










Figure 32 (upper right).

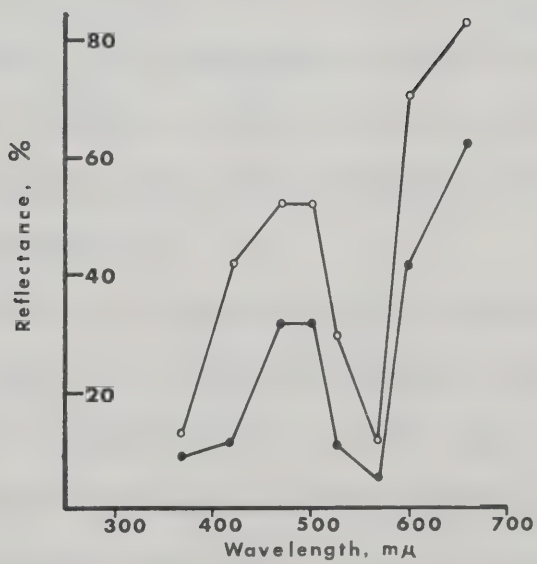
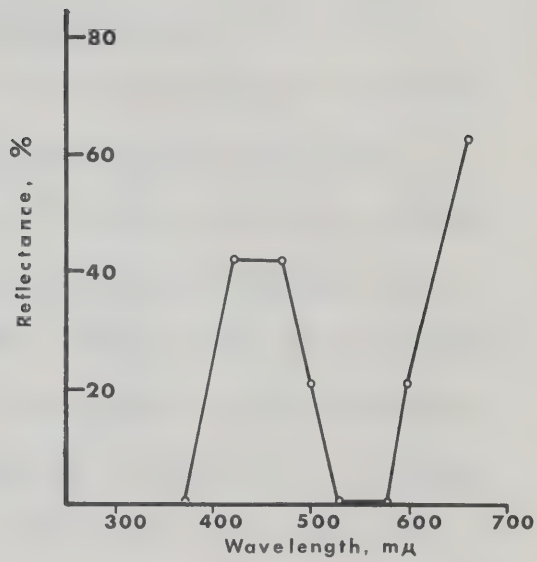
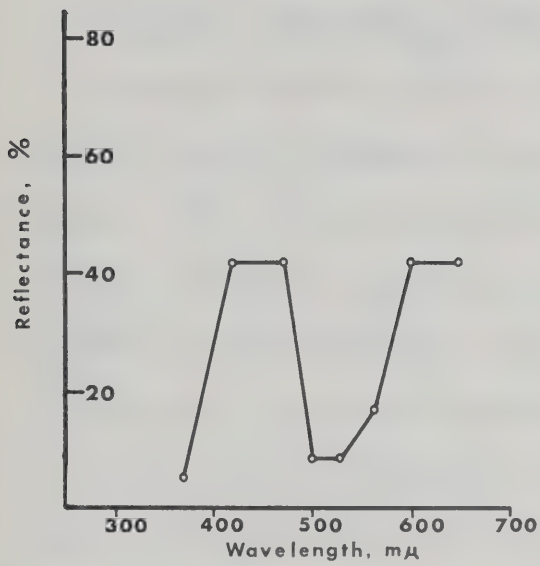
Spectral distribution of reflection from a flower of *Saxifraga oppositifolia*. (Pollen (not shown) is yellow.)

Figure 33 (upper left).

Spectral distribution of reflection from a flower of *Erysimum Pallasii*.

Figure 34 (below).

Spectral distribution of reflection from a flower of *Pedicularis arctica*. Open circles, lip of flower; closed circles, from side.





in the ultraviolet only (see Appendix I). Table 11 shows the per cent of the Hazen area flowers falling into the various colour categories compared with data from Weevers (1952) and Tikhomirov (1959).

#### V.2.3.3. Discussion of flower colour *per se*

Obviously Weevers' (1952) scheme of the percentage of variously coloured flowers throughout the world does not hold good in the arctic. White flowers are particularly in excess, while red, violet, and blue flowers are more scarce; yellow and purple flowers occur in about the same frequency in the Hazen flora as they do in the rest of the world. One cannot extrapolate information on the pollination of flowers without knowing about ultraviolet reflection. As Weevers points out red flowers are often associated with bird pollination, but flowers such as red poppies reflect ultraviolet and are cross-pollinated by insects. The information available at present points to flaws in Weevers' scheme, but does not allow any detailed treatment because of the paucity of world wide information on the exact wavelengths reflected by flowers.

Some generalities can be applied. White flowers reflect little or no ultraviolet light (e.g. *Cerastium alpinum*, *C. arcticum*, *Polygonum viviparum*, *Cassiope tetragona*, *Draba* spp., etc. and the ray florets of *Erigeron compositus*, *E. eriocephalus*, and *Chrysanthemum integrifolium* in the Hazen area flora. This is because of the anthoxanthin compounds which absorb ultraviolet strongly (Weevers, 1952). Yellow flowers may or may not reflect ultraviolet, but if they do it is never over the entire surface (*Ranunculus sulphureus*, *Saxifraga Hirculus*, *Arnica alpina*, *Pedicularis capitata*); in these flowers



Table 11.

Number and per cent of species reflecting various colours of light at Hazen Camp compared with Weevers' (1952) data for Sweden and the world, and Tikhomirov's (1959) data for Taimyr.

<u>Flower colour</u>	<u>No. species</u>	<u>%</u>	<u>% Sweden</u>	<u>% world</u>	<u>% Taimyr</u>
green	2	3.6	8	7.5	
white	32	54.2	26	26.5	40.5
yellow	23	38.9	33	31.0	33.3
red-pink	3	5.1	13	15.0	} 9.6
purple	4	6.8	4	7.0	
violet	1	1.7	11	7.0	12.5
blue	0	0	6	5.5	2.2
UV	6	8.5	-	--	--
<hr/>					
Total species:	59		1350	18,000	156
					Tikhomirov (1959)
Total per cent:		118.8	114		





ultraviolet reflection forms a pattern. From my data no generalities can be drawn for the other coloured flowers, ultraviolet patterns may or may not be present (e.g. see Appendix I). On flowers of *Epilobium latifolium* the veins reflect ultraviolet to the same extent as the rest of the petal, but absorb more radiation in longer wavelengths. Patterns of red or orange on yellow are found on the delicately spotted petals of *Saxifraga tricuspidata* and *S. Hirculus*. The most complex pattern of colours is found on *S. Hirculus*. This flower's petals distally are coloured yellow+ultraviolet (insect-purple, see below), about half way along their length ultraviolet reflection ceases except for that from two small raised swellings quite near the base of the petal, the rest of the proximal area of the petals is yellow with orange spots (Figs. 25 and 26). Mosquin (1969) has generalized that ultraviolet reflection is more common in heterostyled flowers, of which there are none in the Hazen flora.

#### V.2.4. Leaf Colours with Respect to Insect Colour Vision

From Fig. 35 it can be seen that leaf colours are quite variable. Although they appear green to us a number of them reflect ultraviolet, and as such appear more or less white, or grey to insects. The results presented here are confused by differential colouring over leaves, their pubescences, shiny cuticles, and overall low reflectances. The leaves generally reflect less than 50% of the light impinging on them at any wavelength, and average about 15% (within the albedo values given by Nekrasov (1958) and McKay *et al.* (1970)). These low reflectances make it difficult to assign exact colours to the leaves. However, suffice it to say that they are generally dull greens, yellow-greens,

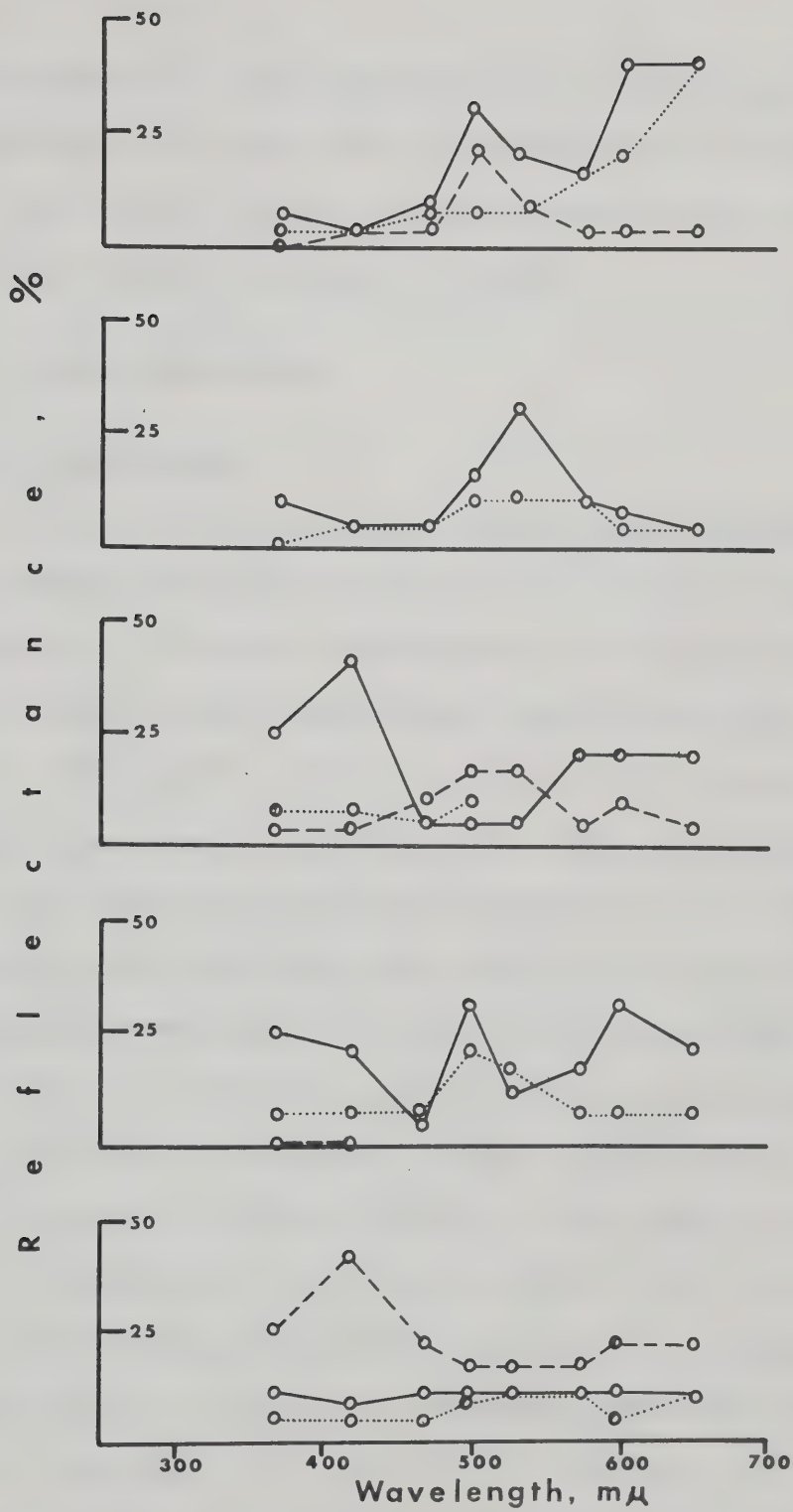




Figure 35.

Spectral distribution of reflection from leaves of different plants. From top to bottom at shortest wavelength

solid line	<i>Pedicularis arctica</i>
dotted line	<i>Saxifraga oppositifolia</i>
broken line	<i>Pedicularis capitata</i>
solid line	<i>Ranunculus sulphureus</i>
dotted line	<i>Epilobium latifolium</i>
solid line	<i>Saxifraga tricuspidata</i>
dotted line	<i>S. Hirculus</i>
broken line	<i>Potentilla nivea</i>
solid line	<i>Stellaria longipes</i>
dotted line	<i>Dryas integrifolia</i>
broken line	<i>Erysimum Pallasii</i>
broken line	<i>Lesquerella arctica</i>
solid line	<i>Salix arctica</i>
dotted line	<i>Cerastium alpinum</i>





and yellows; or, in terms of insect vision, insect-greys to insect-dull-greys.

This consideration of the background against which flowers bloom is important for an examination of the saturation of the colours of flowers, the contrast they have with the vegetative parts around them, and their relative visibilities to insects.

#### V.2.5. Insect Colour Vision

##### V.2.5.1. Introduction

Recent reviews of this subject by v. Frisch (1960), Goldsmith (1961) and Burkhardt (1962, 1964) point out the similarity of the spectral sensitivity of insects, particularly in the ultraviolet. The majority of work in this field has been done with honey bees (*Apis mellifica* L.). Klühn and Pohl (1921) repeated the earlier honey bee training experiments done by von Frisch (1913, 1914), but considered ultraviolet, and demonstrated that bees are sensitive to it. Klühn (1927) showed that the honey bee's visual spectrum is entirely shifted towards the shorter wavelengths: he demonstrated that they distinguish as colours ultraviolet (300-400 mμ), blue (400-480 mμ), blue green (480-500 mμ), and yellow (500-650 mμ), as well as transitional colours. Daumer (1956) developed a technique whereby he could exclude or measure the effects of brightness and saturation of colours. From this he measured the relative stimulation caused by each colour; having assigned the arbitrary value of 1 to green, he found that orange had a relative value of 0.3; blue-green, 0.5; yellow, 0.8; blue-violet, 1.5; and ultraviolet, 5.6. With this information he devised a trichromatic colour scheme for honey bee colour vision; 55% yellow plus 30% bee





violet plus 15% ultraviolet make 'bee white'. In doing this he cleared up a lot of earlier confusion. He concluded that honey bee colour vision has 6 principal colours. Electrophysiological studies by Autrum and von Zwehl (1962, 1963, 1964) and Autrum (1965) dovetail very closely with this.

#### V.2.5.2. Insect colour vision: experimental at Lake Hazen

##### V.2.5.2.1. Aims

The aims of these experiments were to determine spectral discrimination ranges of some of the common anthophilous insects at Hazen Camp in relation to flower colours and field observations on their flower visitations, and to determine the extent to which visual attraction to flowers is brought about by their colours.

##### V.2.5.2.2. Materials and methods

My method relied on positive phototaxis. The insects were introduced into a multilateral visiometer similar to that described by Yinon and Shulov (1966), but adapted for field work.

The apparatus consisted of a large nonagonal central chamber 44 cm across. Into each side was inserted a cardboard tube with an inside diameter of 5.0 cm. On the end of each tube was affixed one of the filters already described (Fig. 5, Table 10) arranged in the following order clockwise around the visiometer: 18A, 61, 48, 87, 608, 25, 65, 35, 626. Bright sunshine was used as a light source. Each experiment was repeated four times with different quarters of the visiometer pointing towards the sun. This was done to offset any effects of brighter illumination entering the tubes on the sunny side



of the visiometer. The whole apparatus was installed inside a polyethylene hothouse during experiments. The heat inside kept the insects active and the polyethylene film diffused the light. The spectral transmission of the 4 mil polyethylene film is given in Table 12.

Table 12.

Spectral transmission of 4 mil polyethylene film (J. Murray, Canadian Industries Ltd., Plastics Technical Center, Brampton, Ont., pers. comm.).

<u>Wavelength mμ</u>	<u>Transmission, %</u>
300	48
350	49
400	54
450	59
500	63
600	68
650	69

Each experiment lasted for  $\frac{1}{2}$  hour, after which the insects at each filter were counted and the numbers recorded. The insects used were: Calliphoridae *Boreellus atriceps*; Muscidae *Spilogona* spp., *Scatophaga apicaulis*, *Fucellia pictipennis*; Culicidae *Aedes impiger*; *A. nigripes*; Empididae *Rhamphomyia nigrita*, *R. filicauda*.

#### V.2.5.2.3. Results

The results obtained are given in Table 13 but do not lend themselves to detailed treatment because of the crude nature of the experiments. The filters do not have exactly equal transmissions, filters 18A, 35, 25, 608, and 87 being transmitting more light than the others, and 626 transmitting the least. Some compensation in the ultraviolet and violet wavebands was no doubt afforded by the polyethylene film of the



Table 13.

Insect spectral sensitivity at Hazen Camp as determined by preference to different wave bands in a multilateral-visiometer.

		Wave Band (μm)									
		300- 400	350- 450	400- 500	450- 550	500- 600	550- 650	600- 700	650- 750	750- 850	Number
<i>Spilogona</i> spp.	%	64.8	27.4	0*	1.8	5.3	0.7	0	0	0	115
<i>Fucellia pictipennis</i>	No.	8	6	0	0	0	1	0	0	0	15
<i>Aedes</i> spp.	%	18.9	17.3	12.1	12.8	13.0	10.1	2.7	6.4	4.4	135
<i>Aedes</i> spp.	%	12.4	14.2	14.8	21.4	25.9	3.5	5.2	1.4	0.7	259
<i>Rhampomyia</i> spp.	No.	14	5	0*	0	1	1	1	0	1	23
<i>Scatophaga apicalis</i>	No.	0	0	0	0	1	0	0	0	2	3

\* Insects attracted here if no shorter wave band filters available.





greenhouse. I have made no attempt to apply any corrections, for the transmissions of the filters, the direction of the sun, or arrangement of the filters. The results can be treated qualitatively only.

#### V.1.2.5.2.4. Discussion and conclusions

The spectral range of vision of the insects studied at Hazen Camp does not vary from that generally thought to be representative of the insects generally. That is, insects can see from ultraviolet through yellow and orange-red; from 300 mμ to 650 mμ (*cf.* von Frisch, 1960; Goldsmith, 1961).

Within the range of the insect visual spectrum, there are differences in preference (Weiss, 1943, 1944; Goldsmith, 1961) and in sensitivity (Burkhardt, 1964; Daumer, 1956), some according to physiological state (Ilse, 1928, 1937). Generally insects show highest response to ultraviolet and violet, with a trough in the blue, and a second peak in response in the green to yellow part of the spectrum. My data show this for the Calliphoridae, Muscidae, and Empididae. The exception appears with the Culicidae, particularly in the second experiment. Studies on the colour vision of mosquitoes conflict in their results (Clements, 1963). It is likely that such insects exhibit different colour preferences at different stages of development. Nevertheless my results show responses in the ultraviolet through red, and both show maxima, either primarily or secondarily, around the yellow part of the spectrum. Another exception is found in *Scatophaga apicaulis*, which may be photonegative in going to the infrared filter, however there is too little data to offer any theory meaningfully. Bumblebee colour vision has been touched upon by Mazokhin-Porshnyakov



(1962) who shows that they have a visual range very similar to that of honey bees, and proposes a trichromatic scheme for them in the range of 365 mμ to 630 mμ. I placed several workers of *Bombus polaris* in the visiometer, but they wandered around inside, apparently disorientated.

#### V.2.6. Flower Colour and Insect Colour Vision

Flower colour has long excited interest from the point of view of insect attraction. Lubbock (1881) concluded that blue was the honey bee's favourite colour. Plateau (1899, 1900 a,b) and others studied flower colours and their role in insect attraction, but came to no conclusions about preferences. He says (1899)

"les Insectes se chargent eux-mêmes de nous montrer que toutes les couleurs des corolles ou des inflorescences leur sont parfait indifférentes, du moment que ces mêmes corolles ou inflorescences contiennent soit le nectar, soit le pollen cherché."

Clements and Long (1923) present an excellent résumé of the work on flower colour and insect attraction, and point out the shortcomings and contradictions in it. They conclude that colour is important for insect attraction, but wisely do not mention overall preference of one colour for all insects. They comment on specific instances of colour preference, and say of bees:

"In field and garden, differences in color are of great importance in attraction, but the bee discriminates among them only when it is to its advantage to do so,..."

Faegri and van der Pijl (1966) do not attempt to draw any generalities about flower colour and insect attraction either.

Nevertheless, colours distinguish flowers of some species from those of other species. This, of course, is very important to insects.



For this reason, I have presented the colours of the flowers in the Hazen Camp study area on a trichromatic colour scheme for bees as proposed by Daumer (1956) which I have extended to include the majority of diurnal anthophilous insects. This is compared with the flower colours as they appear on a trichromatic colour scheme for humans as given by Wright (1944).

One point needs clarification when relating my work to that of Daumer (1956). Daumer used artificial light and has not considered sunlight. His data are presented in terms of the amount of energy necessary in each wavelength to produce "Bienenweisz." In nature surfaces which appear white to humans reflect all wavelengths in the human visual spectrum equally well. Thus one would expect 'Bienenweisz' to reflect all the wavelengths in the bee's visual spectrum in proportion to the amounts of energy being emitted by the sun in those wavelengths; and that the bee's eyes will respond in proportion to this energy. This proves indeed to be the case as can be seen from Table 14.

Table 14.

Bee white (Bienenweisz) as established by Daumer (1956) and per cent of energy in each colour band to cause equal stimulation in honey bees (Daumer, 1956) and per cent distribution of energy in each colour band emitted from the sun and falling on the earth's surface (List, 1968).

<u>Wavelength</u> <u>mμ</u>	<u>Bienenweis,</u> <u>%<sup>1</sup></u>	<u>Equal stimu-</u> <u>lation<sup>2</sup> by %</u>	<u>Solar white<sup>3</sup></u> <u>% total energy</u>
300 - 390	15	14.9	16.45
410 - 480	29.75	29.8	29.95
500 - 650	55.25	55.2	54.20

1 From Daumer (1956).

2 Calculated from Daumer (1956)

3 Calculated from List (1968)





This fact allows me to treat my data exactly as I have taken it from the films, that is in terms of a white reference in each waveband. The two trichromatic representations for flower colours, are given in Fig. 36 for insects and Fig. 37 for humans, as related above.

In the following discussion I have decided to depart from Daumer's (1956, 1968) colour naming scheme in which he introduces a number of special insect colours, namely 'bee-violet' and 'bee-purple', in conjunction with names which we as humans attach to colours. Instead I have called what we see as yellow, 'insect-red'; what we see as blue, 'insect-green'; ultraviolet as 'insect-blue'; etc. I think this removes confusion from the colour system, and at the same time contributes to the understanding and appreciation of colours as insects might see them. Thus the names of the colours are given according to human colour vision, and merely preceded by the word 'insect' to designate to which trichromatic scheme I am referring, in reference to human colour vision no prefix is attached to the name of the colour.

The first thing one sees upon examining the two trichromatic representations of the colours of the entire Hazen Camp flora is that there is a far greater spread of flower colours for the insects, occupying some 60% of the area of the triangle, as opposed to only 45% for human colours. The second is that the colour classes of the flowers are far more distinct, and in no case overlap in the insect colour scheme; whereas for humans there is considerable overlap in the purple-mauve-pink area (E, F, and G) and in the white-yellow area (W, L, and B). The third thing one notices is that there are more colour classes in the insect scheme than in the human scheme, by 12 to 9. All this must surely mean that insects must be able to







Figure 36.

Trichromatic representation of Hazen Camp flower colours for insect colour vision as proposed for honey bees by Daumer (1956).

Key to letters:

A	-	green
B	-	yellow
C	-	red
D	-	orange
E	-	purple
G	-	pink
H	-	light green
J	-	red-purple
M	-	yellow-green
N	-	light yellow-green
P	-	pink-orange
Q	-	blue-green
W	-	white

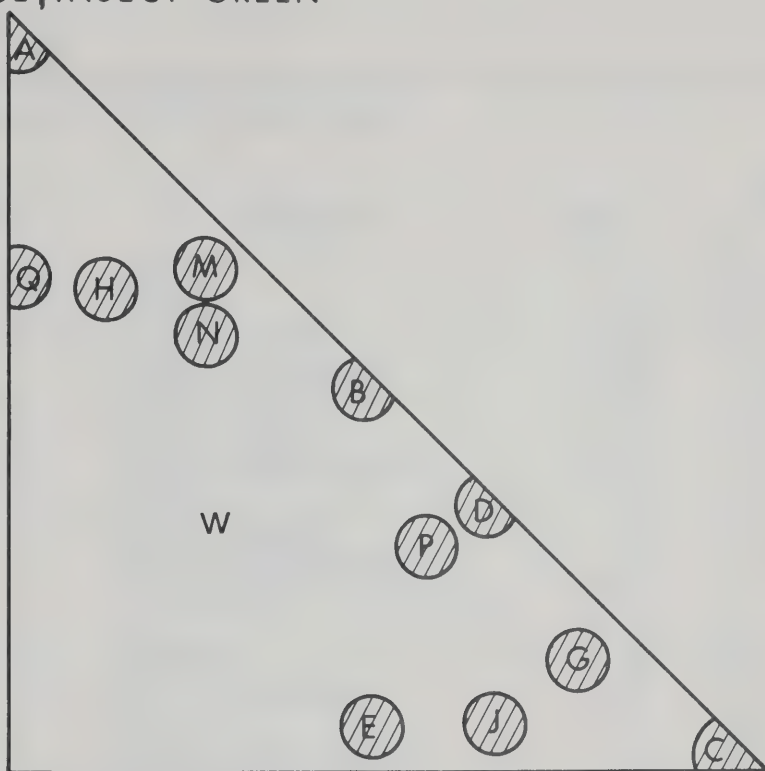
Figure 37.

Trichromatic representation of Hazen Camp flower colours for vertebrate (human) colour vision.

Key to letters:

as in Fig. 36.		
L	-	light yellow
K	-	red-orange
F	-	mauve, light purple

BLUE, INSECT GREEN



ULTRAVIOLET, INSECT BLUE

YELLOW, INSECT RED

GREEN

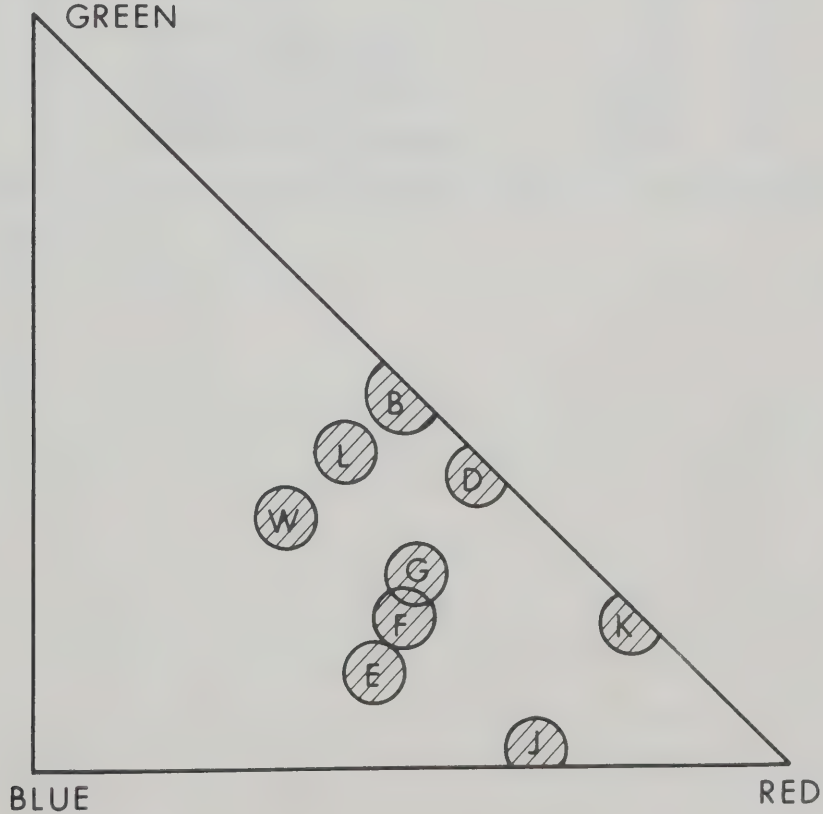




Table 15.

Per cent and number of flowers of the Lake Hazen flora in each colour class for insects and humans.

Insects		Colours	Code	Human	
%	no.			%	no.
0	0	white	W	41.9	18
41.9	18	yellow	B	23.3	10
7.0	3	yellow + red	B+C	0	0
		yellow + orange	B+D	2.3	1
0	0	yellow + white	W+B	2.3	1
0	0	light yellow	L	9.3	4
0	0	light yellow + red	L+C	2.3	1
4.7	2	green	A	0	0
2.3	1	yellow-green	M	0	0
4.7	2	light yellow-green	N	0	0
2.3	1	light green + blue green	H+Q	0	0
18.8	7	red	C	0	0
4.7	2	orange	D	0	0
0	0	white + orange	W+D	2.3	1
0	0	purple	E	4.7	2
0	0	mauve, light purple	F	2.3	1
2.3	1	pink, red-pink	G	4.7	2
4.7	2	red + mauve	C+E	0	0
0	0	red-purple	J	2.3	1
4.7	2	red + red-purple	C+J	0	0
0	0	white + red-orange	W+K	2.3	1
2.3	1	orange + black	D+Blk	0	0
2.3	1	pink-orange + orange	P+D	0	0
Total		43			43





recognize flower colour classes more readily and with greater ease than an animal with trichromatic colour vision similar to that of humans.

The detailed analysis of the flower colour for the Hazen Camp flora is presented in Appendix I. From an examination of this material several more classes of flowers can be erected on the basis of colour, the extra classes result from the number of two-tone flowers of which there are only 5 with respect to human colours, but 10 for insects. This presents to insects an array of 17 different colours and combinations of colours of flowers all very distinct from one another, as against the 14 less distinct colours and colour combinations for ourselves (see Table 15).

### V.3. The Colour Saturation of Flowers and Entomophily

Colour saturation is the percentage of light reflected in the dominant waveband within the spectrum of sensitivity of the sensor; here the insect eye. There have been many comments made about the brightness of white crepuscular flowers, the dullness of some green and reddish flowers pollinated by flies, and the intense colours of arctic and alpine flowers. However, the saturation of colours of flowers has received little attention in pollination ecology. The studies by Daumer (1956) and Mazokhin-Porshnyakov (1959) allow some analysis, and these authors have considered the reflectance of the vegetative parts of the plant in comparison with the flowers. In the arctic many early naturalists regarded the flowers as very bright, but there has been no measurement. Mosquin and Martin (1967) remark that *Astragalus alpinus* was not visited by flies probably because



its purple flowers have about the same reflectivity as the adjacent greenery.

The colour saturation in the insect visual spectrum of the flowers around Hazen Camp is given in Appendix I. Of the 11 yellow\* flowers and 19 white\*\* examined, all have saturations between 65% and 85%. The pink to purple<sup>+</sup> flowers have low saturations at about 45%, the exception is *Epilobium latifolium* which is slightly brighter (53% saturation). The dullest inflorescences are those of *Melandrium apetalum* and female *Salix arctica* (stigmas)<sup>++</sup> at about 10% saturation each.

Most leaves are dull, only 3 of 13 examined reaching 45% saturation within the insect visual spectrum (then in the ultraviolet). They average about 15% saturation, some showing primary or secondary peaks (from 20-35% saturation) in the green (see Fig. 35). Some of these values may be artificially high in leaves with shiny cuticles.

Thus white and yellow inflorescences stand out as considerably brighter than the surrounding vegetation. Pink and purple flowers although contrasting less against their background vegetation are

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\* Includes insect-purple inflorescences and male *Salix arctica* catkins because of the masses of yellow pollen. Excludes white flowers with yellow centers (i.e. *Erigeron* spp. and *Chrysanthemum integrifolium*).

\*\* Includes white flowers with yellow centers.

<sup>+</sup> These have saturations about 65% in the red (exception: *Saxifraga oppositifolia*; 45% saturation outside the insect visual spectrum.

<sup>++</sup> The saturation of the pubescence of both staminate and pistillate catkins is low (ca. 10%).



quite differently coloured. The notable exceptions are pistillate catkins of *Salix arctica*, flowers of *Melandrium apetalum*, and the anemophilous flowers of *Oxyria digyna* and probably *Armeria maritima* and monocotyledons.

#### V.4. Flower Outlines and Sizes in Relation to Entomophily

Pleiomorphy is a highly developed flower state (Leppick, 1956, 1957a, b), but does not necessarily result in greater attractiveness of the flowers to insects; in fact they may be outdone in this respect by actinomorphic forms. This is because the compound eyes of insects are stimulated according to the proportion of facets being used to form the image. It has been demonstrated in bees (Zarrahn, 1933) and butterflies (Ilse, 1932) that there is greater preference for highly divided figures than for uniform figures of the same size. Manning (1956b) suggests that it is the contrast of the petal colour and the background which attracts insects, and the longer the line of contrast in the insects' (honey bees') visual field the more attractive are the flowers. Flicker fusion must also be involved here. Generally it seems that insects choose forms merely on the frequency of change of retinal stimulation (Wigglesworth, 1965) and so the above may be expanded to include all insects.

The size of flowers must be important in visual attraction. The greater the size of the flower, then the greater the distance over which it is seen by, and attracts an insect. This has been demonstrated in bumblebees (Kugler, 1943). Smaller flowers exhibit less attractiveness generally, but the lower limits of this depends on the visual acuity of the insects concerned. Many of the entomophilous flowers





are formed into cymes, racemes, and spikes and probably function as a unit as in *Pedicularis arctica*, *Polygonum viviparum*, or the flowers may be very close to one another so as to form a compact coloured unit as in *Draba Bellii* and *Saxifraga oppositifolia*.

Several of the early naturalists in the arctic pointed out the apparently large sizes of flowers there. However Tikhomirov (1959) has considered the sizes of Taimyr flowers and points out that only 16% of the 118 plants analyzed had flowers greater than 2 cm in diameter\*, and that the flowers are no larger, and generally smaller than they are in more temperate regions; they are merely considerably larger than the size of the plant would suggest. He also considers that racemes and mats of small flowers may be important in attracting insects.

#### V.5. Flower Sizes and Outline Lengths at Hazen Camp

##### V.5.1. Materials and Methods

The diameters of the flowers at Hazen Camp were measured with a vernier caliper and their outline lengths calculated. Usually, at least 10 flowers of each species were used.

##### V.5.2. Results

The unbroken outline length (UOL) of the flowers was calculated without regard to divisions (e.g.  $\pi D = \text{UOL}$ ). These circumferences fall into 5 brackets, and the numbers of flowers in each is given in Table 16.

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\* He includes 28.4% of the flora which have small plain flowers and are pollinated by wind.





To gain a measure of the extra stimulative power of these flowers due to their broken outline lengths (i.e. the outline lengths with all the divisions also measured) was determined in terms of resultant multiplication of the unbroken outline length to the nearest 0.5 times. The total broken outline length also takes into account the extra length brought about by dual coloration in flowers. The number of flowers in each is given in Table 16.

Table 16.

Flower and inflorescence sizes and outline lengths for Lake Hazen flora.

Unbroken out- line length (cm) UOL	Class	No. of species	Total (broken) outline length (cm) BOL	Class	No. of species
0 - 1.8	small	1	0 - 1.8	1	4
2.2 - 2.9		2	2.2 - 2.7	2	6
3.4 - 4.7	medium	3	3.3 - 4.4	3	7
5.7 - 7.3		4	5.0 - 8.0	4	13
8.5 -	large	5	14.0 -	5	6

*Pedicularis arctica*, *Salix arctica*, and *Polygonium viviparum* fall into class but defy meaningful measures, they are regarded as large.

#### V.6. Flower Movement and Entomophily

Following from an earlier remark on the attractiveness of flowers depending on the frequency of change of retinal stimulation (Wigglesworth, 1965), it would seem that floral motion might act as an attractant (cf. Faegri and van der Pijl, 1966). In fact Wolf (1933, 1935, 1937) have shown that flowers held immobile were less attractive to bees than those kept in motion. Vogel (1964) has shown that some very small flowers may be almost constantly moving and could attract insects



this way, other flowers have mobile appendages of "Flimmerkörper" to attract insects. At Hazen Camp the flowers move as units, there are no flowers with mobile appendages.

The importance of flower motion has been little studied from the point of view of pollination.

#### V.6.1. Materials and Methods

Observations on the relative movements of flowers in the light breezes on days of insect activity in the Hazen Camp area enabled me to assign to each flower an arbitrary relative category to describe its motion. The observations were carried out when the wind speeds at the heights of the flowers were less than 3 mps, and usually at about 1 mps. The four categories are listed below.

- 1 Stiff: flowers with very little floral motion.
- 2 Mobile-stiff: flowers with a flickering type of motion.
- 3 Mobile: flowers with movement in short strokes, not flickering but not swaying.
- 4 Swaying: flowers with swaying motion in the wind.

#### V.6.2. Results

The results are presented in Appendix I for each species. Table 17 shows the numbers of inflorescences falling into each movement category. The results are almost predictable considering the length, thickness, and form of the stems bearing the inflorescences. Those "stiff" are very decumbent or have thick stems or both. Those "mobile-stiff" have short thin stems, or are taller with thicker stems. Those "mobile" have relatively thin, medium length stems with relatively large flowers. Those "swaying" inflorescences are large and grow atop long thin stems.



Table 17.

Number of species in each floral movement class.

<u>Movement class</u>	<u>No. of species</u>	<u>Examples</u>
1	14	10 spp. of Cruciferae
2	19	<i>Saxifraga oppositifolia</i> & others, <i>Salix arctica</i> , 4 spp. of Cruciferae
3	7	<i>Dryas integrifolia</i> , <i>Epilobium latifolium</i> , <i>Taraxacum</i> spp.
4	6	<i>Papaver radicatum</i> , <i>Melandrium</i> spp., <i>Arnica alpina</i> , <i>Potentilla nivea</i>

V.7. Flower Form and Entomophily

Many systems of flower classes have been proposed, but most have inconsistencies (Faegri and van der Pijl, 1966). From the point of view of visual attraction and recognition of flowers for insects, Leppik's (1956, 1957a, b, 1963a, b, 1968) classification serves usefully. He separates flowers according to their symmetries, starting with amorphic types in which the shape is indefinite, to halpomorphic types which are radially symmetrical, to actinomorphic types which have large numbers of radial axes of symmetry, to pleomorphic forms with reduction of the number of axes of symmetry such that "figure numerals" may play an important role in the recognition of certain flowers by pollinators. Figure numerals are defined by Leppik (1956) as "certain amounts of objects or units arranged symmetrically so that they can be quickly distinguished from one another and easily memorized according to their definite form." Stereomorphic flowers are those in which depth effects, or three dimensional qualities come into play. His





final class is the zygomorphic type of flower, possessing bilateral symmetry. Faegri and van der Pijl (1966) feel that the last two classes are too broad. This may indeed be the case when considering all flowers, but at Lake Hazen the paucity of these two classes make Leppik's system adequate.

Leppik (1953) states that bees can distinguish from 1 through 6, and 8, 10, and 12; and that their favorite form numeral is 5. It is generally established that many insects can recognize forms and visual markers (Wigglesworth, 1965). In anthophilous insects form numerals may be important, as has been suggested for honey bees (Hertz, 1935; Leppik, 1953, 1955) some tropical butterflies (Leppik, 1935, 1956), stingless wild bees (*cf.* Schwarz, 1948), and bumblebees (Kugler, 1942, 1943; Werth, 1949).

#### V.7.1. Flower Forms and Figure Numerals at Hazen Camp

In the Hazen Camp area amorphic and halpomorphic flowers are absent. However, in some plants flowers growing closely together so that they touch each other and form mats or club-shaped inflorescences. The former I have designated a secondarily amorphic as the shape of the mat, although tending to be hemispherical, is irregular. Examples are *Draba Bellii*, *Saxifraga oppositifolia*, and *Silene acaulis*. The latter growth form I have designated rhopalomorphic (Greek *rhopalos* = club). Examples from Hazen Camp are inflorescences of *Salix arctica*, *Polygonum viviparum*, *Erysimum Ballasii*, *Pedicularis arctica*, *P. hirsuta*, and *P. sudetica*. Clearly the growth form of the inflorescence is sufficiently regular to warrant their separation, just as the inflorescences of Compositae, although having zygomorphic florets, are obviously



actinomorphic secondarily.

These group inflorescences which act as the attractive unit to insects are termed "anthia" by Faegri and van der Pijl (1966: 21) and their importance has been recognized in the arctic by Tikhomirov (1959).

Most of the arctic flowers are pleomorphic. At Hazen Camp steriomorphism is developed weakly in such flowers as *Cerastium* spp., *Saxifraga* spp., and some Cruciferae; moderately in some Cruciferae (i.e. *Draba* spp., *Braya* spp., and others), and is well developed in *Melandrium* spp., *Erysimum Pallasii*, *Cassiope tetragona*, and *Silene acaulis*. Only the last 5 strongly stereomorphic flowers are not included within the pleomorphic group. Within the Cruciferae around Hazen Camp everything from weak (*Lesquerella arctica*) to very strong stereomorphy (*E. Pallasii*) is found.

Zygomorphic flowers are represented best by *Pedicularis* spp.

Table 18 shows the numbers of inflorescences falling into each form with figure numeral considered where relevant.

#### V.8. Honey Guides on the Lake Hazen Flowers

Sprenkel (1793) first noticed visual honey guides on the corollas of flowers in which nectar is hidden. They are more frequent on zygomorphic flowers (Muller, 1881) but do occur on other flowers also. Kugler (1930) discovered that of 356 bumblebee-flowers, 179 were zygomorphic, and of these 60 had honey guides; of the remaining 177 flowers only 24 were so equipped. Generally visual honey guides contrast with the basic petal colour, but may be simply variations in the saturation of the basic colour. Manning (1965a) found that they are often



Table 18.

Numbers and some examples of inflorescences from Hazen Camp in each form with figure numerals given where relevant.

<u>Flower form</u>	<u>No. of species</u>	<u>Figure number</u>				<u>Examples and Comments</u>
		<u>4</u>	<u>5</u>	<u>8</u>	<u>10</u>	
Amorphic	0	-	-	-	-	
secondarily	3	1	2	0	0	Mats of flowers
Haplomorphic	0	-	-	-	-	
Actinomorphic	0	-	-	-	-	
secondarily	5	-	-	-	-	Compositae, only <i>Taraxacum arctogenum</i> included
Pleomorphic	31	15	11	2	3	
Stereomorphic strong	5	1	3	0	0	Figure number for <i>Cassiope</i> is 5, but not relevant to insects, <i>Melandrium</i> spp., <i>Erysimum Pallasii</i>
medium	-	15	-	-	-	Cruciferae
weak	-		7	-	4	
Zygomorphic ( <i>s. strictu</i> )	9	-	-	-	-	Compositae (as above), <i>Salix arctica</i>
to insects	3	-	-	-	-	<i>Pedicularis</i> spp. (excl. <i>sudetica</i> )
Rhopalomorphic	5	-	-	-	-	<i>Salix arctica</i> , <i>Polygonum viviparum</i> , <i>Pedicularis arctica</i> , <i>P. hirsuta</i> , <i>Erysimum Pallasii</i>





consisted of converging lines which produce the maximum flicker effect.

Closely associated with visual honey guides may be scented honey guides (Lex, 1954; Manning, 1965a) which Bolwig (1954) has demonstrated to form patterns on the petals. The mid veins of the petals may smell more strongly than or differently from other veins, and gradients of smell may exist within the flowers (Lex, 1954). With such a scented honey guide insects could find nectar by the topochemical sense.

At Hazen Camp there are few flowers which present honey guides. No ultraviolet honey guides were found, ultraviolet patterns seem only to add to the overall distant attractiveness of the flowers possessing them. The flowers showing honey guides are *Cerastium alpinum* and *C. arcticum*; *Saxifraga Hirculus*, *S. tricuspidata* and *S. caespitosa*; and possibly *Potentilla Vahliana*.

In the *Cerastium* spp. the honey guides are present as two translucent lines on each petal. In the *Saxifraga* spp. the honey guides are present as spots of orange or red, or insect-black or dark red on light yellow, insect-red, petals. *Potentilla Vahliana*, an insect-red flower, has an insect-dark-red base on each petal. Some other flowers show differential coloration at the base of the petals, but such are not considered important or really valid.

It is worth noting that most of these guides are the same colours, that is insect-dark-red to black on an insect-red background, and as such may be relatively inconspicuous and serve little or no function in these flowers. Kugler (1936) has shown that red-marked flowers of *Aesculus hippocastanum* are not well visited by bees.

I have no evidence that any of the honey guides noted above serve





a useful function, as none of the flowers are particularly entomophilous. Insects seen visiting them did not appear to orientate in relation to them, and certainly large visitors, particularly bumblebees do not need them. The two ultraviolet, reflecting spots on the petals of *S. Hirculus* (that is purple on red for insects) may aid the small *Parasitica* in finding nectar within these flowers, but this can be of little use to the flowers.

Structural honey guides have received little attention. I propose that the strong convolutions in the lips of *Pedicularis* species may function as honey guides as they point to the small opening in the galea through which insects must probe to reach the deep seated nectaries. I watched, on one occasion, a female mosquito (*Aedes* sp.) at Hazen Camp run its proboscis up the median convolution in the lip of a flower of *P. arctica*, and insert it into the tube; of course its proboscis was too short for it to be successful in obtaining a meal. I have also watched *Boloria* feeding at the same species of flower successfully, and it too fumbled its proboscis on the labellum before inserting it into the corolla tube. The most abundant visitors to *Pedicularis* spp. are the *Bombus* spp. which may well learn by the convolutions in the labellum the way to extract the abundant nectar of these flowers; experienced bumblebees work too fast to observe this in the field but some indication of this can be seen from the cinematographic sequences of *Bombus* spp. on *P. canadensis* presented by Macior (1967, 1968). The smaller visitors to *Pedicularis* flowers almost certainly follow the convolutions on the lip to gain entrance to the corolla tube. The lips of *Pedicularis* species at Hazen Camp are more saturated in colour than the rest of the corolla.



In *Stellaria* spp. the entire petals may function as honey guides to the small Parasitica often found with their heads into the nectar at the base of the petals.

The smallness of the flowers (the largest 'flowers' are the inflorescences of the Compositae) in the arctic make honey guides unnecessary, except for the very smallest of insects, which can be of little importance in pollination even if it were necessary in the flowers they visited. Larger visiting insects have no trouble finding the open nectar supply. Only in the zygomorphic flowers of *Pedicularis* spp. is there any need for a honey guide, and I have demonstrated that such exists in the form of convolutions on the lip.

#### V. 9. Flower Odours and Entomophily

Odour is a well known attractant for insects and may function over long distances, particularly in small, amorphic, inconspicuous, or crepuscular flowers, as well as in flowers producing imitative odours. Most flowers produce odours which are probably detectable by insects over short distances and function to provide extra sensory information to visual stimuli on the close approach of the insects to the flowers, thereby enticing the insect to land (Butler, 1951; Manning, 1956 a, b, 1957). These short range odours are not strong and are generally 'absolute' odours (cf. Faegri and van der Pijl, 1966) which have "-- to man -- ... no direct, immediate counterpart outside the sphere of blossoms." Much of the early work on the role of odour in pollination is reviewed in Clements and Long (1923).

The sense of smell in insects is very diverse according to the biology of the insect considered (Hocking, 1960; Dethier, 1963;





Wigglesworth, 1965). Interestingly, honey bees appear to have very similar senses of smell to man, not only in the compounds sensed, but also in the threshold concentrations needed (Schwarz, 1955). Probably all anthophilous insects can detect the odours of flowers.

#### V.9.1. Flower Odours in the Arctic

Observations on the odours of flowers in the arctic are very confused, and contradictory. Very often arctic flowers are considered to have no scent, with a few exceptions (Mosquin and Martin, 1967) or almost the opposite is held (Ekstam, 1895, 1897; Fridolin, 1936). Even so, it seems that scent is reduced in arctic flowers. This has been attributed to the large size of the flowers, a wrong supposition as has already been shown (Tikhomirov, 1959); and to the perpetual daylight making strong scent redundant in the face of colour (Aurivillius, 1883).

#### V.9.2. Flower Odours at Hazen Camp

At Hazen Camp a study was undertaken to discover which flowers are scented, and at which state of their development in terms of anthesis and nectar production scent could be detected.

Flowers picked in the field on days of insect activity were simply sniffed. At the same time, notes were taken on the development of the flower, the presence or absence of nectar or pollen, and the weather. It was realized that the observers could detect different strengths of odour and an arbitrary scale of 0-4 was agreed upon, flowers rated 0 had no odour even when the flower was warmed in a tube in one's pocket; and 4 were considered relatively (for the study area) quite odoriferous.





### V.9.3. Results

The results for the species considered are given in detail in Appendix I from which Table 19 has been extrapolated. Of the 42 species examined 32 species were scented. Two were considered strongly odoriferous, *Erysimum Pallasii* and *Arnica alpina*, both of which are listed by Mosquin and Martin (1967) as apparently scentless. *Arnica alpina* is very odoriferous on warm sunny days. I could smell the flowers while standing amongst them at Gilman Camp.

Table 19.

Numbers of inflorescences falling into each odour class and criteria for each class.

<u>Odour strength</u> <u>class</u>	<u>Scale criterion</u>	<u>No.</u>	<u>Comments and</u> <u>examples</u>
0	no smell	10	6 Cruciferae
1	slight smell	10	
2		11	
3		9	
4	strong smell	2	<i>Erysimum Pallasii</i> <i>Arnica alpina</i>

The odours of most Hazen flowers are similar and were thought of as sweet. The exceptions are *Melandrium* spp., *Chrysanthemum integri-*  
*folium* and *Erigeron* spp., *Taraxacum* spp., and *Cassiope tetragona*. The *Melandrium* spp. had the typical smell of campion which pervaded the taste of the nectar; *C. integriolium* and *Erigeron* spp. had smells best described as daisy-like; and *C. tetragona* had a heathy-sweet scent which Hocking (1968) records as "sweet-aromatic." Hocking also recorded *Silene acaulis* scented similarly to *Melandrium* spp., but I did not note this.



#### V.9.4. Flower Odour and Insects

The only insects I am sure use odour for examining the state of flowers are bumblebees and possibly Syrphids. These insects were quite frequently noted to hover in front of flowers that had attracted their attention. In one day I noticed 3 workers of *Bombus (Alpinobombus) polaris* hovering in front of *Dryas integrifolia* flowers, as if inspecting, before flying on and hovering in front of another blossom upon which they landed and took nectar. Syrphids were noted hovering in front of any intended flower, and were usually seen to land. I am unsure that this behaviour was in response to scent as it was seen in front of even the most food laden scented inflorescences of staminate catkins of *Salix arctica*, and the most unlikely, unscented flowers of *Draba groenlandica*. Other insects, Tachinidae, Calliphoridae, Muscidae, Empididae, Culicidae, and Lepidoptera were observed to fly straight to the flowers, from distances up to 3 meters and land before investigating for food. This indicates that visual stimuli probably are the chief cues to attraction. Once on the flowers all insects use the topochemical sense to locate food.

#### V.10. Attraction by Convection Currents from Flowers

This topic has not been touched upon before. There is very little data to support the idea that convection currents serve as attractants. In mosquitoes Howlett (1910) demonstrated attraction because of convection currents rather than radiation, and carbon dioxide was needed in the currents to initiate responses in *Aedes aegypti* (Burgess, 1959).

In flowers convection currents must be generated by the heat gained by the flower from the sun, and even if these themselves do not attract



insects, the currents must take off the odour of the flowers and extend the short range attraction due to odour. This must be particularly noticeable to insects on warm sunny days when the flowers are warmed considerably, and are producing most odour.



## PART VI

### REWARDS FOR THE INSECTS

#### VI.1. Pollen as Insect Food

Faegri and van der Pijl (1966) state that there is good reason to consider pollen the original attractant for insects to flowers. Pollen is used as food particularly by bees, some beetles; a few flies, particularly Syrphidae, are well known pollen eaters. Downes (1955) describes the ceratopogonid, *Atrichopogon pollinivorus*, sucking out the protoplast of individual pollen grains of *Prunus lusitanica* and honeysuckle. Bee larvae eat the whole grain and digest the protoplast by diffusion through the micropylar membranes (Whitcomb and Wilson, 1929; Faegri, 1962) as do some Collembola (Kevan and Kevan, in press) and the syrphids and muscids found to have eaten pollen.

Very little attention has been paid to the importance of pollen in the nutrition of insects other than honey-bees. Lubliner-Mianowska (1956) and Lunden (1954) have reviewed the literature on aspects of pollen chemistry, the latter author including works on allergens. It is difficult to generalize about the nutritive values of different pollens as they differ widely in their chemical composition. Protein content varies from 8.6% to 45.37% (Lubliner-Mianowska, 1956) and averages over 25% (Lunden, 1954). Conifer pollen, well documented collembolan food, is lower in protein content at about 16%. The essential amino acids show less variation (*cf.* Auclair and Jamieson, 1948; Weaver and Kuiken, 1951; Lunden, 1954). Todd and Bretherick (1942) found carbohydrates (sugars and starches) to make up about 25% of pollen extracts. Lipids and other ether extractable materials





are in very variable amounts, ranging from 1-20% (Hügel, 1962) with a mean about 5%. Interestingly, pollens of *Brassica* spp. (Cruciferae) and *Taraxacum* spp. are rich in lipids (Todd and Bretherick, 1954). The vitamins in pollens are diverse and of different concentrations (Lunden, 1954). Other pollen constituents reported by the above authors are pigments, enzymes, co-enzymes, minerals, as well as undetermined materials or ash.

Clearly pollen is a highly valuable food, providing all the basic nutrients for any animal able to use it.

In the arctic, some work has been done on the pollen loads of *Bombus* spp. (Hoeg, 1924, 1929, 1932; Richards, 1970) and pollen feeding Diptera have been observed (McAlpine, 1965; Mosquin and Martin, 1967; Hocking, 1968).

#### VI.1.1. Pollen Availability at Hazen Camp

*Taraxacum hyparcticum* is the only showy inflorescence which does not produce any pollen (Porsild, 1964), *Arenaria rubella*, *Polygonum viviparum*, and *Taraxacum arctogenum* produce very little pollen, all the Cruciferae produce some pollen as do the remaining flowers. By far the greatest pollen producers are *Salix arctica*, *Saxifraga oppositifolia*, *Papaver radicatum*, *Dryas integrifolia*, *Potentilla nivea*, and *Epilobium latifolium*.

#### VI.1.2. Pollen Feeding Insects, with Reference to Hazen Camp

Pollen feeding is not widespread among insects. The most notorious pollen feeders are probably bees and some beetles. Of the families of insects common to Hazen Camp pollen feeding has been recorded in the following: Entomobryidae (Kevan and Kevan, in press), Ceratopogonidae



(Downes, 1955, 1958), Empididae (Lovell, 1898; Porsch, 1966; Downes, 1969), Dolichopodidae (Laurence, 1953), Syrphidae (Müller, 1873; Knuth, 1906; McAlpine, 1965b; and others), Muscidae (McAlpine, 1965b), Cordyluridae (Knuth, 1906; McAlpine, 1965b), possibly Tachinidae (McAlpine, 1965b), Calliphoridae (Knuth, 1906), Bombidae, and a dubious record of Chironomidae (Hocking, 1968). Of these, only the Entomobryidae, Syrphidae, Muscidae, Cordyluridae, Tachinidae, and Bombidae have been recorded with any certainty as eating pollen from flowers around Hazen Camp.

All 15 of the collembolans (*E. comparata*) examined from the flowers of *Lesquerella arctica* at Hazen Camp had ingested pollen grains. The grains appeared unbroken. Attempts to age and sex these animals were not successful so that no correlation between their pollen feeding in their "sensitive period" (Shelford, 1963) and their physiological state was possible (see IV.4).

The relationships between the flower visits of the Syrphidae and their biologies can be explained. *Phalacrodira nigropilosa* was the first syrphid to appear in 1967. Both males and females appeared simultaneously early in the season and both (5 of each) fed on pollen; only 1 male and no females were found without pollen in their guts. The inflorescences from which pollen was eaten were *Salix arctica* and *Saxifraga oppositifolia*. Twenty other specimens were collected but not examined. Of the females dissected 2 had ovarian follicles on stage 1, one at stage 3, and the other 2 were badly damaged and had crushed ovaries. *Carposcalis carinata* appears shortly after *P. nigropilosa*. In this species the males emerge first; the sex ratio being 22 males :10 females until about 20.VI.1967 after which



it became 7 males: 20 females. Only 1 male of 22 dissected, and only 3 females of 25 dissected did not contain pollen. Table 20 shows the distribution of the stages of ovarian follicular development in females on flowers and it is apparent that they feed on pollen throughout their adult lives. They appear to feed on pollen more when the ovarian follicles are at stage 2 and yolk deposition is just starting, but more adequate sampling is needed to prove this. My tentative explanation for the seasonal change in sex ratio of pollen feeding insects is that the males emerge first and require pollen to mature their gonads in time to mate as soon as, or soon after, the females appear. Both sexes fed on pollen from inflorescences of *Salix arctica*, *Saxifraga oppositifolia*, *Dryas integrifolia*, *Erysimum Pallasii* (1 male, 1 female), and possibly *Potentilla* sp., *Papaver radicum* and *Lesquerella arctica*. Because the females emerge later and remain active longer they feed more extensively on *D. integrifolia* than the males.

Both sexes of *Metasyrphus chillcotti* eat pollen. I collected 2 males and 1 female with pollen in their guts; 1 male was without pollen, and 4 other females were not dissected, 1 of these was watched as it tried to feed from the undehisced anthers of a flower of *Saxifraga oppositifolia*. They also fed from inflorescences of *S. arctica* and *D. integrifolia*. I did not record *Helophilus borealis* eating pollen, though undoubtedly it does (cf. Hocking, 1968).

From the muscoid flies McAlpine (1965b) describes a male of *Scatophaga nigripalpis* and 5 females of *Pogonomyoides segnis* feeding on the pollen of *Dryas integrifolia*. I found no *Scatophaga* spp. feeding on pollen but I recorded 15 females of *P. segnis* which had ingested pollen, 7 females and 6 (all) males which did not contain







pollen. McAlpine (*l. cit.*) records 1 male imbibing nectar only. Table 21 shows the distribution of the follicular development in females. It appears that they eat pollen throughout their adult lives, with the possible exception of when the ovarian follicles are at stage 1, at which time these flies may still be pupae (*cf.* Chironomidae and Oliver, 1968). It seems that males do not feed on pollen. This strengthens the idea that the females of this species use pollen for ovarian maturation. Of 8 female specimens of *Eupogonomyia groenlandica*, only 1 had pollen in its gut and had ovarian follicles at stage 3. Neither of the 2 males dissected contained pollen. One female specimen either of *E. groenlandica* or *P. segnis* was collected with pollen in her gut and ovarian follicles at stage 4. The flowers used by these two species were mainly *D. integrifolia*, and possibly *Potentilla* sp. and *Arnica alpina*. Among the *Spilogona* spp. I collected only 2 with solid material resembling pollen grains in their guts, 1 was a female of *S. tundrae* or *S. dorsata* with ovarian follicles at stage 4, and the other was probably *S. melanosoma*.

The pollen requirement of *Bombus* spp. are reviewed in Part IV. Neither Richards (1970) or I saw newly emerged over-wintered queens eating pollen (*cf.* Free and Butler, 1959). The results given in Tables 8 and 9 and the subsequent discussion adequately demonstrate the correlation between colony development and pollen requirements for developing broods at Hazen Camp.

#### VI.2. Nectar in Relation to Insects

Faegri and van der Pijl (1966: 53-55) discuss the origins of nectaries and nectar. They say that "nectar is apparently something



Table 20.

Distribution of ovarian follicular stages in females of *Carposcalis carinata* with and without pollen in their guts (from Hazen Camp, 1967).

<u>Ovarian folli- cular stage</u>	<u>Number with pollen in their guts</u>	<u>Number without pollen in their guts</u>
1	4	1
2	11	1
3	3	0
4	6	1
spent	0	0
?	1 (poss. stage 1)	0
Total	25	3

Table 21.

Distribution of ovarian follicular stages in females of *Pogonomyoides segnis* with and without pollen in their guts (from Hazen Camp, 1967).

<u>Ovarian folli- cular stage</u>	<u>Number with pollen in their guts</u>	<u>Number without pollen in their guts</u>
1	0	1
2	5	3
3	4	0
4	5 (6)	1
spent	0	0
?	1	2
Total	15 (16)	7

Number in parentheses includes specimen not separated from *E. groenlandica* (see text).



new," (compared with the long history of pollen) "and is in the main peculiar to angiosperms" and in almost all cases is for the attraction of animals. Nectaries may be present on several extra-nuptial parts of plants (in axils, on petioles, bracts, leaves) (Bonnier, 1879) or on almost any part of a flower (Lovell, 1950; Bonnier, 1879), or both. Insect visitors to floral nectaries are well known, and extra-nuptial nectaries also provide sugar for a wide variety of insects (Zimmerman, 1932; Knoll, 1928; Downes, 1968). Nectaries usually consist of closely packed meristematic cells (Bonnier, 1879) and the nectar usually modified phloem sap (Beutler, 1953; Lüttge, 1960).

Many authors (Kerner, 1902; Knuth, 1906; Müller, 1873; Percival, 1965; Meeuse, 1962; and others) have shown that floral and extra-floral nuptial nectaries are located so that most visiting insects must brush against the anthers to feed on the nectar. Thus the dehiscence of the stamens of many flowers faces the source of nectar and is introrse.

Some aspects of nectar chemistry are considered by Beutler (1953) and Percival (1965). The sugars present are mostly sucrose, fructose, and glucose; and sometimes smaller quantities of raffinose, maltose, melibiose, trehalose, and melezitose (Wykes, 1952a); *Berberis* nectar is pure saccharose (Percival, 1962). The proportions of the major sugars varies greatly from family to family, but is more or less constant at the species level (Percival, 1962). The composition of nectar may influence insect visitors. Wykes (1952b) found that honey-bees prefer a mixture of about 1 glucose : 1 fructose : 1 sucrose.

Acceptance threshold concentrations for two calliphorids and the





honey-bee for different sugars are given by Dethier (1963: 138), for other insects (not necessarily anthophilous) (Wigglesworth, 1965: 247-252) and for the butterflies *Pyrameis atalanta* L. (Weis, 1930), *Pieris rapae* L. (Verlaine, 1927), and *Vanessa indica* (Takeda, 1961). Dethier (1963) and Wigglesworth (1965) discuss taste in insects. Most common sugars are acceptable to almost all insects studied including the Collembola (Strebel, 1932). In anthophilous insects the acceptance threshold concentration is well below 10% for most of the common nectar sugars.

Despite apparent preferences, most sugars in nectar are about equally effective in prolonging life because most nectar feeders have enzymes allowing them to use these sugars (*cf.* Hocking, 1953; Wigglesworth, 1965; Salama, 1967; and others). Thus nectar composition is probably not important when considering available energy alone.

Concentrations of sugars in nectar, presented by a number of authors, vary between 2.5% and 87% (Hocking, 1953) but are generally between 28% and 78% (Faegri and van der Pijl, 1966). Concentration, as well as composition, of sugars affects the survival of honey-bees (Vogel, 1931); as it does mosquitos (Salama, 1967). Honey-bees must imbibe nectar of at least 18% sugars if they are not to "work at a loss" (Pryce-Jones in Percival, 1965).

The actual quantities and concentrations of nectar produced are affected by numerous factors which are outlined by Wykes (1951, 1952a); Beutler (1953), Hocking (1953, 1968), Percival (1965), Shuel (1967). Some of these factors are relative humidity, temperature, daily range of temperature, time of day, solar radiation, altitude, latitude, slope, soil minerals, soil moisture, position of the flower or floret on the





plant, age of the flower or floret, incidence of nectar removal, pollination, chemical fertilizers, and even thunderstorms.

The overall significance of nectar as insect food is well established by Elton's (1966) treatment of 'Natural Fuel Stations', which clearly establishes the importance of nectar for insect dispersal. Hocking (1953) writes

"It is not generally realized what a large proportion of adult insects are almost dependent on this plant secretion (nectar). These probably include most of the Diptera, Hymenoptera, and Lepidoptera, a considerable number of Coleoptera, and a few smaller groups from several other orders. Nectar must have tremendous significance in the dispersal of these species." (p. 247).

#### VI.2.1. Nectar as Insect Fuel in the Arctic, with Reference to Hazen Camp

The majority of the work done on nectar secretion in the arctic has been carried out by Hocking (1953, 1968). He found that at Churchill, Manitoba (58° N.); nectar production on the tundra was 3½ times that of the forest in terms of gm sugar/acre/season, and that the concentration of nectar was higher on the tundra (50% sugars) than in the forest (42% sugars). Hocking points out that northern biting flies obtain the energy for flight almost exclusively from floral nectar, and some insects may carry up to 2.17 times their basic weight in nectar held in their crops. The peaks of nectar production in both the tundra and forest regions coincide with the peaks of flight by female mosquitoes, and some species were found swarming with full crops of nectar. At Hazen Camp Hocking (1968) reports that nectar yield in mg sugar/flower/day was higher than at Churchill in 8 of 10 species occurring at both localities but that nectar production per unit area was substantially



less. He records 33% of the insect fauna associated with flowers, but that there is a surplus of nectar produced. He maintains that there is competition between flowers for pollinators rather than among pollinators for nectar. Slope has an effect on the secretion of nectar in *Dryas integrifolia*, *Pedicularis capitata*, *Saxifraga oppositifolia*, and *Salix arctica* (staminate catkins). It is greater on south facing slopes because of the greater insolation.

Although Hocking's work provides valuable insight into nectar secretion, his method of covering flowers with truncated vented cones such as I also used as insect excluders (but for pollination experiments) has shortcomings. I found that these cones acted as small greenhouses and attained temperature elevations in excess of 10 °C in sunny weather, and even 1 or 2 °C under overcast conditions. The high temperatures and higher saturation deficiencies inside these cones may have substantially affected the volumes of nectar secreted and the concentrations measured (*cf.* Beutler, 1953; Hocking, 1953; Shuel, 1967). To obtain reliable absolute results, nylon marquisette tents would be necessary.

I made some measurements of nectar concentrations and volumes from some uncovered inflorescences and present these for comparison, these with those from Hocking (1968) in Table 22. Table 22 shows that of 10 species examined, 3 showed nectar concentrations higher under normal conditions than under experimental conditions; the remaining 7 show concentrations within the range given by Hocking (1968). I did not take sufficient volume measurements to make the more meaningful comparison of the amount of sugar present.



Table 22.

Nectar concentration ranges in % sugars from some Lake Hazen flowers (not covered) in 1966, 1967, and 1968 compared with data from Hocking's (1968) covered flowers.

Plant	Nectar concentration		No. of observations	Nectar concentration		No. of observations
	range of sugars % (this study, not covered)			range of sugars % (Hocking, 1968)		
<i>Salix arctica</i> (male) (female)	27 - 70		19	10 - 64		58
	20 - 78		30	12 - 58		51
<i>Stellaria longipes</i>	65 - 70		20	24 - 55		26
<i>Melandrium trifolium</i>	26 - 27		2	5 - 52		31
<i>Erysimum Pallasi</i>	25 - 38		7	29 - 58		23
<i>Saxifraga oppositifolia</i>	52 - 84		15	21 - 69		42
<i>Dryas integrifolia</i>	40 - 48		5	5 - 77		124
<i>Epilobium latifolium</i>	22 - 36		9	11 - 71		32
<i>Pedicularis capitata</i>	32 - 71		5	42 - 69		33
<i>P. arctica</i>	45 - 65		38	22 - 73		72
<i>P. hirsuta</i>	47 - 67		5	38 - 71		14







It is, however, worth ranking the flora according to the amounts of sugar produced, based on Hocking's study and my own observations. The results fall into 5 categories as presented in Table 23.

I recorded over 110 species of arthropods on flowers at Hazen Camp. Of these, the vast majority were feeding on nectar, but not necessarily exclusively. Those not feeding on nectar were the 4 species of Acarina, the 5 species of Araneida, *Apatania zonella*, and lepidopteran and other larvae. The collembolans, *Entomobrya comparata*, although watched feeding on pollen grains of *Lesquerella arctica*, may also have been imbibing nectar. Most adult Lepidoptera around Hazen Camp probably feed on nectar, and 11 of the 19 possible species were observed doing so in 1967. In the Noctuidae, *Anarta* (*Hadena*) *richardsoni* and *Crymodes* (*Apamea*) *exulis* females are scarce on flowers reflecting their reluctance or lack of need to fly and the greater activity of the males which seek them out; I propose that this lethargy the females exhibit is the first stage towards greater lethargy and brachyptery in some other Lepidoptera (Downes, 1964): *Lasiestra leucocycla* shows no disparity in the number of each sex imbibing nectar from flowers. All 5 species of Rhopalocera were watched imbibing nectar from flowers.

Among the nematocerous Diptera, nectar feeders are not numerous. None of the Hazen trichocerids have been found on flowers and only one dubious record of a tipulid possibly feeding on nectar was made. Chernov (1966) notes that in the Soviet arctic, at Anabarski inlet, 5 species are sometimes found in large numbers in association with flowers. Among the Chironomidae, Oliver (1968) remarks that only



Table 23.

Hazen nectar producers ranked (extrapolated from Hocking (1968), and this study).

Abundant Nectar

*Salix arctica*  
*Saxifraga oppositifolia*  
*Dryas integrifolia*  
*Epilobium latifolium*  
*Pedicularis capitata*  
*P. arctica*  
*Arnica alpina*

Plenty of Nectar

*Melandrium triflorum*  
*Cerastium alpinum*  
*Stellaria longipes*  
*Erysimum Pallasii*  
*Lesquerella arctica*  
*Potentilla nivea*  
*Silene acaulis*  
*Pedicularis hirsuta*  
*Saxifraga tricuspidata*  
*Arnica alpina*

Some to Little Nectar

*Melandrium apetalum*  
*Cerastium arcticum*  
*Arenaria rubella*  
*Braya humilis*  
*Androsace septentrionalis*  
*Polygonum viviparum*  
*Saxifraga Hirculus*  
*Cassiope tetragona*  
*Draba Bellii*  
*Erigeron compositus*  
*Chrysanthemum integrifolium*  
*Taraxacum arctogenum*

Very Little or No Nectar

other Cruciferae

No Nectar

*Papaver radicatum*  
*Oxyria digyna*  
*Saxifraga caespitosa*  
*Ranunculus* spp.  
(*R. sulphureus* unknown)



the adults of 2 species (*Smittia velutina* and *S. polaris*) have been observed imbibing nectar and feels that all others probably do not feed as adults, listing 9 species which refused nectar. Together Hocking (1968) and I have recorded more than 14 species of chironomids from flowers; of these the following feed on nectar: *Limmophyes* sp. or spp., *Smittia velutina*, *S. polaris*, *S. sp.* or spp. (not *velutina*), *Corynoneura* sp. *scutellata*, and *Paraphaenocladus despectus* (all Orthocladiinae). In all species nectar feeding is restricted to the females and almost entirely to inflorescences of *Saxifraga oppositifolia*, *Salix arctica*, *Pedicularis arctica*. The exception is *Corynoneura* sp. *scutellata* most of which were found on *Stellaria longipes*. None of these species is listed among the 9 which Oliver (1968) found to refuse nectar. Ovarian follicles could be found at almost any stage of development in each mentioned species. In *Limmophyes*, stage 2 predominated, in *S. velutina* and *S. spp.*, stage 3 predominated as was true of *P. despectus*; I have too few observations to generalize about *C. sp. scutellata* as only 2 specimens were dissected (one at each of stages 3 and 4). Ovarian follicles at stage 1 were uncommon, being found only in *S. velutina* where they are interpreted as part of further ovarian cycles. The lack of stage 1 ovarian follicles and the predominant later stages probably reflect the fact that adults emerge with their ovarian follicles already on the way to maturation (Oliver, 1968). It is noteworthy that all but *C. sp. scutellata* are early emerging species and are hence restricted to inflorescences in bloom at that time, i.e. mainly *S. oppositifolia* and *S. arctica*. These nectar feeding chironomids must derive nutrition from nectar for mating, ovipositing, and possibly further egg maturation. The other species





found on flowers I think are there purely incidentally, very few of each species were recorded, and no activity other than resting was noted. It is likely that they settle out of the air during cool spells, particularly at night and during cloud, the former condition for settling is probably reflected in Hocking's (1968) remarks on the peak of activity of insects on *Dryas integrifolia* around midnight, "particularly on the part of the lower flies" and "Nematocera between 22.00 and 06.00 hours." If this is true, then this incidental settling is hardly visitation or a peak of activity.

Some Ceratopogonidae are well known nectar feeders (Downes, 1958) and I have recorded most, if not all, the species from the Hazen Camp area from flowers, of which at least two are presumed to have been feeding on nectar. Both sexes of both species of Culicidae from the Hazen Camp area are well documented nectar feeders, and visit flowers throughout their adult lives. No mycetophilids were collected from flowers at Hazen Camp. Of the sciarids I collected 20 specimens of at least 6 species, most of which were observed imbibing nectar of a variety of inflorescences. Both sexes feed on nectar; the females and probably the males, at any stage of their adult lives. Ovarian follicular stages ranged from 2 to 4, none were found at stage 1 and none spent. The females probably emerge with their follicles already partially developed. No cecidomyiids have been recorded imbibing nectar from flowers in the Hazen Camp area.

The Brachycera (*sensu lato*, including Cyclorrhapha) contain most well known flower visiting and nectar feeding flies. I found very few Dolichopodidae on flowers, and recorded only one male of *Dolichopus dasyops* imbibing nectar; nonetheless both species of Hazen dolichopodids





probably feed on nectar. Three species of Empididae were seen imbibing nectar, *Rhamphomyia ursinella* was not. Females of the 3 species commonly found on flowers visit at all stages of their adult lives, *R. nigrita* had ovarian follicles predominantly at stage 2, *R. filicauda* predominately at stages 2 and 3, while *R. hoeli* predominantly at stage 3. This may reflect slight differences in the time of readiness to form swarms for mating in each species, as well as indicating fuel requirement for searching for oviposition sites. On flowers, females are far more abundant than males; the female to male ratios being 145 : 52 for *R. filicauda*, 29 : 6 for *R. hoeli*, 25 : 9 for *R. nigrita*. This may reflect their greater body weights and nutritional requirements in active flight of females. No phorids were collected. All 4 syrphid species feed on nectar. I have interpreted their physiological ages and activities according to pollen feeding. The arguments presented their dove-tail closely with expected fuel demands for flight. Although few piophilids have been collected from flowers 3 species have now been recorded imbibing nectar. I recorded one instance of an agromyzid, *Phytomyza erigerontophaga* apparently imbibing nectar, and do not discount the probability of the 4 specimens I saw on the flowers of its host plant *Erigeron compositus* doing so. Two of the 3 calliphorid species have been observed imbibing nectar and the third, *Protocalliphora sapphira* is uncommon and likely to feed on nectar. *Boreellus atriceps* females visit flowers at all stages of their lives, as no doubt do males. Females with ovarian follicles at stage 4 predominante, perhaps in response to fuel requirements for greater weight. Although *B. atriceps* and *Protophormia terraenovae* visit flowers throughout the summer, they are far more common early on inflorescences of *Saxifraga oppositifolia*



and *Salix arctica*. This may be because they have just finished overwintering and require a sugar meal before going in search of other food. Of the 4 species of tachinids collected from flowers at Hazen Camp, 2 were watched imbibing nectar. *Peleteria aenea* was common on *Arnica alpina* at Gilman Camp. Males outnumbered females 12 to 6 and all females dissected had ovarian follicles late in stage 3. It is likely that most of the tachinids around Hazen Camp imbibe nectar.

Of the muscoids at least three species of *Scatophaga* have been collected on flowers. Both sexes of *S. apicaulis* visit flowers but males more so than females (13 : 6), both are also predators. In the Anthomyiinae only *Fucellia pictipennis* (both sexes) were found feeding on nectar, particularly from *Saxifraga oppositifolia*. Despite the commonness of this insect only 12 specimens have been recorded on flowers at Hazen Camp. *Pegomyia* sp. or spp. have rarely been collected on flowers and *Hylemyia fasciventris* Ringd. not at all at Hazen Camp. Both species of Phaoniinae are well documented nectar feeders, females of *Pogonomyoides segnis* feed extensively on pollen while *Eupogonomyia groenlandica* rarely, if ever, eats it. *E. groenlandica* males and females are equally abundant on flowers. Females, and probably males visit flowers throughout adult life, females particularly when the ovarian follicles are at stage 4. In *P. segnis*, females visit flowers throughout their adult lives but at no one stage of ovarian follicular development (although stage 1 was rarely seen). In this species, females far outnumber males (19 : 6) particularly as the season advances. This may be a result of the males' feeding on nectar, finding females, mating, and dying, while the females habit of eating pollen is related to ovarian maturation and nectar feeding supplementary food for flight.





Eleven species of *Limnophorinae* (*Spilogona*) have been recorded from flowers around Hazen Camp and although all have not been seen imbibing nectar I do not doubt that they rely heavily on nectar for fuel for flight. *Spilogona melanosoma*, *S. sanctipauli*, and *S. tundrae* were the most common nectar feeders of their genus at Hazen Camp in 1967. Both males and females of *S. melanosoma* imbibe nectar, but females more frequently (4 : 9) particularly when they are almost ready to lay eggs. Both males and females of *S. sanctipauli* imbibe nectar but in this species males far outnumber females (29 : 11), again the females seem to visit flowers when almost ready to oviposit. *S. tundrae* was far less common, being recorded 6 or fewer times on flowers. Both males and females imbibe nectar.

It is likely that most of the adult Hymenoptera feed on nectar, but few observations of nectar feeding were possible. Nectar feeding has been seen in the following: *Nematus* sp., Chalcidae, *Tetrastichus*, *Tridymus* sp., *Atractodes* sp., *Mesoleptus* sp., *Saotis* sp., *Stenomacrus* sp. or spp., and of course *Bombus polaris* and *B. hyperboreus*. It is likely that given sufficient time, most of the Ichneumonidae would be recorded as flower visitors. Nectar feeding by *Bombus* spp. has been discussed in relation to colony development in Part IV.

### VI.3. Ovarian Tissue and Whole Inflorescences as Food

Damage to the ovarian tissue by pollinators, notably beetles as primitive pollinators, has led to the hypothesis that inferiorly located ovaries have developed for protection (Grant, 1950a, b). The flowers at Hazen Camp are almost entirely with superiorly located ovaries, the exception being the Onagraceae (*Epilobium latifolium*).





Ovarian tissue and sometimes whole flowers are eaten by several lepidopterous larvae, as is shown in Table 24. Hocking (1968) states that "the ovarian tissue of plants is of interest to insects principally as a source of food for the next generation, that is, as an oviposition site." This point is valid for the Tenthredinidae and possibly for the cecidomyiid of unknown food habit on *Salix arctica* (Downes, 1964; and see Part IV). Possibly some of the microhymenoptera are 'parasitic' on the seeds of some plants. Larvae of the noctuid moth *Sympistris labradoris* are restricted to feeding in the flowers of *Dryas integrifolia* where they eat the sporophylls. Adult females of this species may oviposit within the flowers (Hocking, 1968) but it also seems that the caterpillars find their ways into the flowers in subsequent seasons, and that females may lay eggs in association with the plants before the flowers have opened (see Part IV). Another possible flower feeding caterpillar is of *Stenoptilia mengeli* (see Part IV and Imms, 1964). Shamurin (1966a) notes that flowers of many plants serve as oviposition sites and larval food sources of Diptera.

Adult arthropods feeding on the ovaries of flowers, but not exclusively, were species of Acarina from several flowers, see Table 24.

I saw two vertebrate species eating flowers; the willow ptarmigan, *Lagopus mutus rupestris* eating flowers of *D. integrifolia* and *Lesquerella arctica*; and the arctic hare (*Lepus arcticus*) eating flowers of *Melandrium triflorum*, *Erysimum Pallasii*, *S. oppositifolia*, *D. integrifolia*, *Pedicularis arctica* and *P. capitata*.



Table 24.

Arthropods feeding on ovarian tissue of flowers at Hazen Camp, 1967.

<u>Species</u>	<u>Inflorescences</u>	<u>No. of obser- vations</u>	<u>Comments</u>
<i>Cecidophyes</i> sp.	<i>S. oppositifolia</i>	2	
Eriophyidae (undetermined)	<i>S. oppositifolia</i>	2	
<i>Bryobia praetiosa</i>	Cruciferae (8 spp.) <i>Papaver radicum</i> <i>Potentilla</i> <i>nivea</i> <i>D. integrifolia</i>	many some	
<i>Byrdia</i> sp.	<i>Salix arctica</i>	1	
	<i>Dryas integrifolia</i>	1	
<i>Anarta</i> ( <i>Hadena</i> ) <i>richardsoni</i>	<i>S. arctica</i>	6	
	<i>Oxyria digyna</i>	2	
* <i>Sympistris</i> <i>labradoris</i>	<i>D. integrifolia</i>	9	cf. Hocking, 1968
<i>Stentoptilia</i> <i>mengeli</i>		0	possible flower feeder (cf. Imms, 1964)
Noctuidae (undetermined)	<i>S. arctica</i>	1	
	<i>Saxifraga</i> <i>oppositifolia</i>	16	
Lycaenidae (undetermined)	<i>S. oppositifolia</i>	5	
<i>Boloria</i> sp.	<i>D. integrifolia</i>	1	
*Cecidomyiidae	<i>S. arctica</i>		eggs
*Tenthredinidae	<i>S. arctica</i>		eggs

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\* Possibly restricted to ovarian tissue



#### VI.4. Flowers as Sites for Copulation

Shamurin (1966a) says that flowers of many plants in the tundra seem to serve as places for copulation of Diptera. I found 1 pair of *Phytomyza erigerontophaga* copulating on an inflorescence of *Erigeron compositus* and swarms of male and female *Smittia* spp. (probably mostly *velutina*) over patches of *Saxifraga oppositifolia*.

#### VI.5. Death of Anthophiles in Flowers

The first mentioned predator apparently in flowers is the ascid mite *Arctoseius cetratus* of which 10 were collected in flowers of *Saxifraga oppositifolia*. These are free-living predators of nematodes and microarthropods and may have been in these flowers for other mites or purely incidentally. Other mites were found attached to 2 specimens of *Smittia velutina* but proved to be phytophagous Eriophyidae. Two female *Smittia* sp. specimens were found with a mermythid nematode inside. Three cases of muscoids (2 *Eupogonomyia groenlandica* and 1 *Pogonomyoides segnis*) dead from disease caused by the fungus *Entomophthora muscae* were collected from flowers. In the above examples the rôle of the flowers is probably incidental.

In the Araneida, particularly *Xysticus deichmanni*, and 2 insects, *Scatophaga apicaulis* and *Rhamphomyia filicauda* flowers play an integral part in the capture of prey. *Dictyna borealis* has been recorded from 4 species of flowers, never with prey, but in ambush and having built a web; a spider suspected of being this species had captured, killed, and eaten a male of *Spilogona melanosoma* in a web. *Pardosa glacialis* was found on *Salix arctica* catkins. *Tarentula exasperans* may use clumps of *Saxifraga oppositifolia* as ambush sites in the same way as





*Scatophaga apicaulis*. Only one specimen thought to be *T. exasperans* was caught with prey in a clump of *S. oppositifolia*. A single observation was made of *Erigone psychrophila* on a flower of *Dryas integrifolia* under the anthers of which it may have been awaiting prey. In all the above flower visiting is probably incidental. The only spider using flowers habitually is *Xysticus deichmanni*. These spiders use many inflorescences; yellow flowers predominate, purple flowers are used, but white ones apparently never. These spiders are yellowish and may have the ability to assume a purplish tinge when in purple flowers (cf. Wickler, 1968: 54). They do not reflect ultraviolet (at least on an ultraviolet absorbing background) and were not encountered on the distal parts of the ray florets of *Arnica alpina* which reflect ultra-violet. Insects preyed upon were *Carposcalis carinata* (2), muscid (1), *Spilogona* sp. (1), *Rhamphomyia* sp. (1), *R. filicauda* (1), *Mesoleius* sp. (1). Only the adult males of this spider are not carnivorous, and only these, and very young stages too small to attack most anthophilous insects were not found in flowers.

Two males of *Rhamphomyia filicauda* on the same day at different localities had captured prey presumably for their courtship ritual. Males of these flies may use flowers, especially *Dryas integrifolia* as preying sites (see Downes, in press). Prey captured was a female of *Aedes nigripes* and a small chironomid, too mutilated for identification. Hocking (1968) reports a similar single observation for *R. (Dasyrhamphomyia) nigrita* which is known to capture prey in flight (Downes, in press).

*Scatophaga* spp. are well known carnivores and around Hazen Camp *S. apicaulis* (2 males, 3 unsexed) use clumps of flowers, particularly





of *Saxifraga oppositifolia* as prey sites. Insects preyed upon in 1967 were predominantly females of *Phalacrodira nigropilosa* (7 females : 1 unsexed). The remaining record was of *Nematus* sp. as prey to a female on a pistillate catkin of *Salix arctica*.

#### VI.6. Flowers as Havens from Predators

While collecting from flowers I noticed that many insects escaped because my shadow passed over the flower well ahead of my net. This was particularly noticeable in the heliotropic flowers, which usually had to be approached from behind. Flowers also offer vantage points from which resting insects probably detect motion at a distance. These effects can only be applied to protection from predators or potentially dangerous animals which approach, rather than await, their prey. The possible predators involved are *Rhamphomyia filicauda*, and some birds (e.g. Hoary red-poll, *Acanthis hornemanni hornemanni*; willow ptarmigan, *Lagopus mutus rupestris*; knot, *Calidris canutus canutus*, and ruddy turn-stone, *Arenaria interpres interpres*); potentially dangerous animals include herbivores, animals likely to crush vegetation, and entomologists.

#### VI.7. Flower Microclimate and Insects

##### VI.7.1. Introduction and Review with Reference to the Arctic

Knuth (1906 - 1909) considered that some flowers can sometimes offer shelter to a variety of insect visitors. He mentions particularly the Labiatae and the flower bells of *Campanula* offering shelter to insects during rain or at night. Composites too, he says, may be used as night shelters; they close and offer a warm air space



within the flower. However, Blüdel (1959a, b) has demonstrated dandelion flowers are cooler than the temperature of the air around them at night. Knuth also discusses larval protection and food, such as is found in the symbiotic relationships of *Yucca* and the Yucca moth, and of *Ficus* spp. and their gall wasps; both of which develop within the flowers and fruits of their respective plants. Hagerup (1950) writes of an interesting relationship between thrips and *Calluna* in the Faroes. These, with other ethologically analogous interrelationships, are discussed by Faegri and van der Pijl (1966).

Elevated temperatures have been measured within the inflorescences of "pit-fall flowers" since the time of Lamarck (1777, in Cook, 1883). These flowers also offer warm shelters to insects (Knuth, 1906; Judd, 1961) whose roles as pollinators has been described by Faegri and van der Pijl (1968), Meeuse (1922), and others.

Other flowers had not been examined until Krog (1955) working in Alaska, and Blüdel (1958) in Germany measured the temperatures within catkins of *Salix* spp. Blüdel (1956, 1959a, b) considered still other flowers and their microclimates in relation to nectar secretion and apiculture. In the arctic the first hint of the possible importance of elevated corolla temperatures to plants was made by Bonnier and Flahault (1878) who postulated that the darker corollas (and other plant parts) absorbed solar radiation for heat used in assimilation. After Krog (1955), Tikhomirov *et al.* (1960) and Shamurin (1966b) investigated floral microclimates, but not in reference to insects. Hocking and Sharplin (1965) considered for the first time corolla temperatures in relation to flower basking insects in the high arctic, and so presented some arctic flowers as possible "shelter blossoms."





Faegri and van der Pijl (1966), taking a botanical approach, discount the importance of "shelter blossoms" or "Obdachblume" saying:

"Whether shelter blossoms also exist in reality seems rather doubtful." (p. 58)

"The idea of a 'warm shelter' as attractant is hardly tenable, being unnecessary in the tropics, and realized during day-time in fair weather only (when no shelter is necessary) in temperate regions." (p. 71)

#### VI.7.2. Aims

In the following study I will attempt to show that "the idea of a 'warm shelter' is "tenable," and is of great significance to some insects and plants in the high arctic.

The aims of these experiments were to measure the temperature and microclimate in arctic flowers; to determine how this microclimate is generated; to discover to what extent the microclimate is modified by ambient climatic conditions, and to gain some measure of the significance of this microclimate to insects and plants, separately and together.

#### VI.7.3. Materials and Methods

##### VI.7.3.1. Temperature measurements, instruments

###### 1) Thermocouples and potentiometer.

Copper and constantan thermocouples 0.2 mm in diameter and about 1 mm in length were made from a 20 cm length of double stranded copper and constantan thermocouple wire. The insulation was scraped from the terminal 5 mm of the wire intended to be the thermocouple. The two wires thus freed were twisted together, soldered and clipped to give a 1 mm junction. The remaining wire served as leads. Two such thermocouples were joined in series by the constantan wires at the ends distal from the thermocouples. The pair of thermocouples was then





mounted on to copper lead wires which were connected across a Honeywell Potentiometer, Model 2705. This light, portable apparatus proved very versatile in the field. The thermocouples were left silver with solder to measure air temperature rather than radiation. Hocking and Sharplin (1965) used blackened thermocouples.

Thermocouples were tested before use against a mercury thermometer in a water bath from 0 C to 45 C. They generated .04 mv per 1 C change in temperature and no correction factor was needed. In the field the apparatus was tested with one couple in the shade and the other couple in direct sunlight. No appreciable inequality could be measured in the potential difference between the two thermocouples. Thus I feel that the apparatus was measuring air temperatures and not radiation. Also, the small size of the thermocouples allowed them to equilibrate with the air about them rapidly thereby giving fast results.

When measuring intra-floral temperatures, or corolla temperatures as they were in most cases, the reference couple was allowed to hang freely in the air at the same height as the experimental subject and at a distance of less than 5 cm from it. The air temperature was measured at the same position with a previously calibrated Weston Model 2261 dial thermometer (accuracy  $\pm 0.5$  C).

## 2) Thermistors and telethermometer.

a) Bead thermistors (Fenwal BB 32 J1) were wired onto leads and lead into a Yellow Springs Telethermometer, Model 43 TW. The bare bead thermistors have a diameter of .028 inches and were chosen for their short response time and their small size.

Before use, the thermistors and telethermometer were tested against



a mercury thermometer in a water bath from 0 C to 45 C and a correction curve was obtained (Appendix III).

b) In 1968 the above was replaced with a Grant Instruments telethermometer with microprobe thermistors. These probes were tested, and proved to be accurate to less than 0.25 C. This instrument was used extensively for field observations as it is extremely portable, gives excellent service, and needs little attention except for calibration which can be checked on the meter.

#### VI.7.3.2. Inflorescences

The flowers used for experimental work could best be divided into 7 categories. They are 'microgreenhouses', and similarly acting 'hair heat traps'; suspended open 'bells', 'discs', and somewhat similar 'parabolic reflectors', and the 'inverted bells' resembling the latter. Table 25 lists the flowers used according to category.

#### VI.7.3.3. Temperature measurement in inflorescences

Because the six categories of inflorescences are quite different in their mode of generation of microclimate, and because different insects use the warmth in different ways, it is necessary to use different approaches in each of the categories to obtain data which are meaningful.

All experimental results were obtained from flowers mounted on a board and normal to it. The board was attached to a camera tripod so the aspect of the flowers to the sun could be changed in either the horizontal or the vertical planes. This enabled me to simulate a 24 hour period merely by adjusting the aspect of the board. Thus in an experiment taking 20 minutes, I would have from a stationary flower data corresponding to a full day with constant solar elevation.



Table 25.

Flowers and inflorescences used in intrafloral temperature measurements.

Microgreenhouses

*Pedicularis arctica*  
*P. capitata*  
*Melandrium apetalum*  
*M. triflorum*

Hairy heat traps

*Salix arctica* (staminate and pistillate  
catkins)

Bells

*Cassiope tetragona*

Discs

*Taraxacum arctogenum*  
*Arnica alpina*  
*Erigeron compositus*

Parabolic reflectors

*Dryas integrifolia*  
*Potentilla nivea*  
*Papaver radicatum*

Inverted bells

*Saxifraga oppositifolia*  
*Lesquerella arctica*  
*Cerastium alpinum*





When using flowers falling into the categories of parabolic reflectors, inverted bells, and discs, the aspect of the board upon which the flowers were mounted was changed in the vertical plane. An insect pin was stuck into the board and normal to it. The board was then tilted into the sun so that the pin had no shadow; at this point the first readings were taken. Then the board was tilted so that the shadow of the pin was one times, two times, four times, eight times, infinity times the length of the pin, and lost when the pin was tilted into the shade. Table 26 shows the pin shadow length corresponding to the angle of the sun, and the time of day (arbitrarily set in reference to a south-facing flower).

Table 26.

Simulation of one day by shadow length of a pin mounted parallel to the sun's rays, and normal to the substrate (a board) at arbitrary south-facing noon. Shadow length in multiple of pin length, corresponding time, and solar angle of incidence.

<u>Shadow lengths</u>	<u>Solar angles of incidence (°)</u>	<u>Times</u>	
0 times	0.0	12:00	
1 times	45.0	09:00	15:00
2 times	63.5	07:78	16.12
4 times	76.0	06:56	17:04
8 times	83.0	06:28	17:32
∞ times	90.0	06:00	18:00
shaded	90.0 +	06:01	to 18:01





When using bell flowers, microgreenhouses, and hairy heat traps, the aspect of the board upon which they were mounted was changed in the horizontal plane if shading was considered a factor influencing the microclimate within the flowers. In *Melandrium* spp. and *Cassiope tetragona* no changes in aspect were made as shading from other plant parts is negligible. The board was always horizontal and the experimental flowers as they were naturally. For flowers in which shading would influence the temperature (e.g. *Pedicularis* spp. and *Salix arctica*) a simulated 24 hour period of sunshine could be quickly obtained by twisting the board on the tripod, or taking readings of temperature from all around these more or less radially symmetrical inflorescences, or both. Here, as before, in an experiment taking but 20 minutes I had data in a stationary flower or inflorescence corresponding to a full day of solar radiation incident at a constant angle. Table 27 shows the simulated time of day corresponding to the horizontal component of the solar angle of incidence.

Table 27.

Simulation of one day of sunshine by horizontal component of the solar angle of incidence.

<u>Angle (°)</u>	<u>Time</u>
0	12:00 (arbitrary south-facing noon)
45	15:00
90	18:00
135	21:00
180	00:00
225	03:00
270	06:00
315	09:00



The warming and cooling rates of the flowers was measured by taking the temperatures within the corollas after 10 or 15 second time intervals after exposure to and shading from direct insolation at time zero. Temperatures were taken until an equilibrium was reached.

To determine the loss of temperature elevations in *Dryas integrifolia* due to wind, mean wind speeds were recorded at the same time as the temperatures were measured within the corollas of 10 flowers. Wind speed was measured with a wind meter (F.W. Dwyer Mfg. Co.) previously checked against a three cup anemometer.

#### VI.7.3.4. Insects examined

The more common and easily obtainable insects which were found visiting *Dryas integrifolia* had their body temperatures measured under a variety of experimental and natural conditions within and outside corollas. These insects were *Aedes nigripes*, *A. impiger*, *Rhamphomyia filicauda*, *R. nigrita*, *Carposcalis carinata*, and *Boreellus atriceps*. Thermocouples were introduced into the ventral anterior part of the abdomen through a hole punctured with an insect pin. The couple was then pushed forward until it was judged to lie in the thorax, more or less between the flight muscles. This treatment usually killed the smaller insects; however they remained alive long enough for the experiments to be completed. If death occurred sooner the results were disregarded. Larger insects remained active on the thermocouple, gripping the flower they were held in and thereby helping me; some even flew away before experiments were concluded.

Insect body temperatures were taken over simulated 24 hour periods of sunshine in whole, decorollate and desporophyllate flowers. Warming



and cooling rates were also measured.

#### VI.7.4. Results

##### VI.7.4.1. General comment

The data presented in the following pages are subject to immense variation which can only be eliminated and understood by further laboratory studies. In the open environment variation in ambient temperatures; solar energy across the spectrum and in specific wavelengths due to changes in atmospheric transmission according to water vapour and dust, time of day and time of year; and in wind, are not controllable and are difficult to measure. Thus the data are not absolutely comparable between experiments but are comparative in a qualitative and general way.

The experiments are brief and incomplete in places. This is primarily due to inclemencies in the weather. Most of the experiments were done in optimal conditions of bright sunshine, no clouds, no wind. Most of the results of measurements taken on 18.VI.1968, 7.VII.1968 were lost in transit and only ranges and means are available. Nevertheless, I have no reason to doubt that standard deviations, variances, and statistical test results differ in generality from the multitude of other results presented in Appendix III.

##### VI.7.4.2. Microgreenhouse flowers

This group of flowers are those which have enclosed within their corollas a body of trapped air which becomes warmed in direct sunlight. The "greenhouse effect" must augment the heat conserved by the insulating dead air in the corolla. The sporophylls, particularly the pistils,







absorb short wave radiation passing through the translucent corollas, and upon warming reradiate long wave energy which is trapped within the corollas. Similarly short wave heating of the corolla would further supplement the trapped heat, but only from the inner surface. At Hazen Camp microgreenhouse flowers are *Melandrium apetalum*, *M. triflorum*, *Pedicularis capitata*, *P. arctica*, *P. hirsuta*, *P. sudetica*, and also *Salix arctica* (which is discussed separately).

VI.7.4.2.1. *Melandrium* spp.

In the flowers of these species (*M. apetalum*, *M. triflorum*, and *M. affine*) the syncalyx makes a somewhat translucent bulb surrounding the reproductive organs. This bulb acts as a microgreenhouse, elevating the temperature within it. I thought that some insects could make use of such a microenvironment and live off the abundant nectar and pollen produced by these flowers. Thus they were briefly examined.

VI.7.4.2.2. *Melandrium apetalum*

On 17.VII.1968 during optimal conditions and a mean ambient temperature of 15.7 C the temperatures within 11 corollas were measured in the field. The elevations observed had a mean value of 5.2 C. Even in heavy overcast conditions (e.g. 19.VII.1968) the mean elevation above ambient (mean 14.3 C) was 0.7 C (data taken at Tanquary Fiord). Data is given in Appendices III-3-10 to 12.

No insects were ever seen within these flowers.

VI.7.4.2.3. *Melandrium triflorum*

On 7.VII.1968 under optimal conditions at a mean ambient temperature of 14.8 C the mean elevation within 10 corollas was 6.2 C. On 17.VII.



1967 similar results were obtained (mean ambient 17.5 C) when the corolla temperature had a mean elevated value of 4.5 C for 7 corollas. Data are given in Appendices III-3-13 to 16.

Under clouded skies 4 corollas showed a mean elevation of 0.4 C (28.VII.1968). No insects were found within these flowers.

VI.7.4.2.4. *Pedicularis arctica*

On 28.VII.1966 under optimal conditions, 85 intrafloral temperatures were taken for a simulated 24 hours of sunshine at a mean ambient temperature of 10.0 C. These translucent pinkish flowers clearly show the effect of solar aspect. Those flowers with their symmetrical axis normal to the sun's rays having the highest mean temperatures, while those facing the sun are cooler, but by no means as cool as those directed away from the sun. This experiment was repeated a year later (28.VI.1967) under optimal conditions at a mean ambient temperature of 11.5 C. The results from the 72 readings taken on 2 flowers for 4 plants at 8 positions (the readings for directly into the sun being repeated at the end of the experiment) show essentially the same results. The major difference is the much higher internal temperatures found in 1967. The maximum being a mean elevation above ambient of 6.1 C (internal temperature 17.6 C) in the latter but only 1.9 C (internal temperature 11.9 C) in the former. The reason for this difference is unknown. Both sets of data are presented in Fig. 38 and statistical analyses of the differences in Appendix III-3-1, 2.

During cloudy conditions, on 15.VII.1967 and 9.VII.1966 the mean elevated temperature above ambient was 0.8 C for 48 readings (see Appendix III-3-3, 4) and 1.4 for 50 readings respectively.

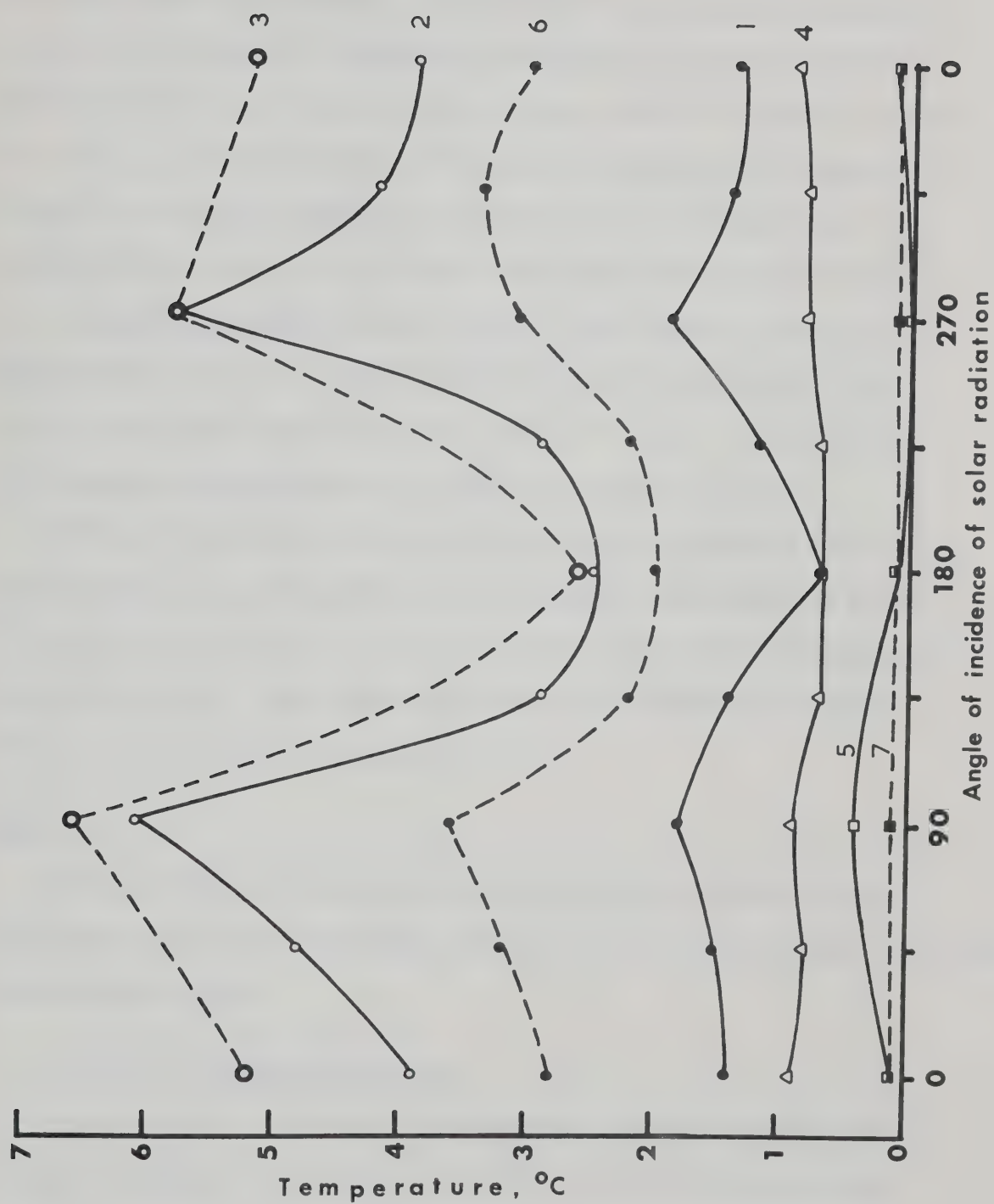




Figure 38.

Mean temperature excesses (C above mean ambient) in *Pedicularis* spp. flowers with respect to the angle of incidence of solar radiation under sunny and cloudy conditions.

Curve 1	28.VII.1966	<i>P. arctica</i> in sunshine	Appendix III-3-1
Curve 2	28.VI.1967	<i>P. arctica</i> in sunshine	Appendix III-3-2
Curve 3	17.VII.1968	<i>P. arctica</i> in sunshine	Appendix III-3-5
Curve 4	15.VII.1967	<i>P. arctica</i> in cloudy weather	Appendix III-3-3
Curve 5	28.VII.1968	<i>P. arctica</i> in cloudy weather	Appendix III-3-6
Curve 6	26.VII.1966	<i>P. capitata</i> in sunshine	Appendix III-3-7
Curve 7	16.VII.1966	<i>P. capitata</i> in cloudy weather	Appendix III-3-8







Data obtained in the field agreed closely with experimental results. On 17.VII.1968 during optimal conditions and a mean ambient temperature of 12.8 C, 10 flowering racemes were divided into quarters according to their aspect to the sun, S facing the sun, and so on round the compass E, N, W, ... From each quarter 20 readings were taken with results compatible with those obtained experimentally, E and W with their symmetry axes of normal to the sun's rays being a mean of 5.8 C and 6.6 C respectively above ambient, while N, away from the sun had a mean elevation of 3.6 C, and S, giving a mean elevation higher than N, but lower than either E or W, at a value of 5.2 C. These results are presented graphically in Fig. 38 and in Appendix III-3-5.

During cloudy weather the elevated internal temperature was all but abolished. On 28.VII.1968 at a mean ambient temperature of 6.3 C; S read 0.1 C; W, 0.4 C; N, 0.1 C; E, 0.0 C; none differed significantly (Appendix IV-3-6). Only within the stem was the temperature warmer, being 7 C at an ambient temperature of 5.5 C.

### Insects

Small insects are quite often found within the corollas. They are notably Chironomids (*Limmophyes* spp., *Smittia velutina*, *Paraphaenocladus despectus* and others).

#### VI.7.4.2.5. *Pedicularis hirsuta*

Flowers of this plant were not examined. They are smaller and a little lighter in colour and must exhibit the same effects as are found in *P. arctica*. *Smittia velutina* and *Limmophyes* spp. have been found within their corollas.



#### VI.7.4.2.6. *Pedicularis capitata*

This plant was treated in the same way as *P. arctica*. On 26.VII.1966 5 plants with 3 of the translucent yellow flowers each were given a simulated 24 hours of sunshine. At a mean ambient temperature of 13.5 C results very similar to those obtained for *P. arctica* were seen. The effect of aspect is less pronounced than in *P. arctica*. The data are presented in Fig. 38 and statistically treated in Appendix III-3-7.

During cloudy weather (e.g. 16.VII.1966) the elevated temperature for 45 readings within the corolla was only 0.1 C (Appendix III-3-8). This was borne out in the field also.

Field observations show that the above effect operates naturally. On 7.VII.1968 the corolla temperatures of 15 flowers was examined under optimal conditions at a mean ambient temperature of 14.0 C. The mean elevated temperature was found to be 17.9 C, almost 4 C above ambient (see Appendix III-3-9).

#### Insects

Despite the fact that these flowers seem to offer the same rewards as the other *Pedicularis* spp. flowers very few insects were found within them. On 17.VII.1966 one specimen of *Limnophyes* sp. was found.

#### VI.7.4.3. Hairy heat-traps

The hairy catkins of *Salix arctica* possibly work in much the same way as microgreenhouses. Krog (1955) examined the catkins of *S. polaris* Walhbg. in Alaska. These became 15-25 C warmer than the ambient air temperature "around freezing." Krog explains the phenomenon saying that the part of the solar spectrum which penetrates the hairs is absorbed



by the dark scales around the flower buds. The heat gained by these scales is largely conserved because of the insulating dead air space within the catkin, and also likely because of the opacity of the shiny hairs to long wave radiation from the heated centre.

"The pussywillow thus forms a 'heat trap' working on the same physical principle as a greenhouse . . ."  
(Krog, 1955)

The phenomenon observed by Krog (1955) and Blüdel (1957) occurred at Hazen Camp in *Salix arctica*. The data obtained from uncut catkins is given in detail in Appendix III-4 for the 3 years of study. Although catkins were mounted on a board and given a simulated 24 hours of sunshine, the data are inconclusive (Appendices III-4-1, 7, 9, 10, 14). Temperature elevations were readily obtained under optimal conditions, but aspect apparently has little effect. This is likely due to the slow cooling rates, and possibly movement of heated air throughout the catkin, upsetting the effect of the rapid changes of aspect in experiments.

#### VI.7.4.3.1. Pistillate catkins

From Appendices III-4-1,2,3,4, and 7 there are obvious statistical significant differences in the temperatures from the insolated side to the non-insolated side during sunny weather. The maximum temperature elevation recorded was 8.5 C, nowhere near the figures presented by Krog (1955). During cloudy weather this effect is abolished and catkin temperatures fall to near ambient, as they do when artificially shaded (Appendices III-4-6, and 15).

#### VI.7.4.3.2. Staminate catkins

These show the same effects as female catkins but to significantly







lesser extents (Appendices III-4-1, 2, 8, 11). The maximum temperature elevation recorded was 7.0 C. Temperatures on the insolated and non-insolated sides may or may not be significantly different (Appendices III-4-9 to 14). During cloudy weather or artificial shading, catkins cool to near ambient (Appendices III-4-8 and 15).

#### VI.7.4.3.3. Differences between pistillate and staminate catkins

It is interesting that in two experiments when both male and female catkins were set up together in sunshine the females were significantly warmer than the males only on the insolated side. The reason for this may lie in the difference in the thickness of the pubescence on the catkins, 3.6 mm in the pistillate but 3.1 mm in the staminate, and in the difference of the density of the pubescence. The shallower and sparser pubescence in the male would allow greater internal circulation of air, and greater heat loss to the outside; the latter explaining the lower values found in male catkins. This has important implications concerning the greater usefulness of heat to pistillate catkins for pollen tube growth and seed development, while in staminate catkins pollen is shed beyond the pubescence and the anthers are subject to the extra heat only early in their development.

During cloudy weather no differences could be detected.

#### Insects

Insects are frequently found deep within the pubescence of both staminate and pistillate catkins. They are mainly chironomid females (*Metriocnemus ursinus*, *Smittia velutina*, *Lymnophyes* spp., *Prosmittia nanseni*, *Paraphaenocladius despectus*, and others) are often found on pistillate catkins, together with yellow eggs possibly of *Nematus*



sp. attached to various parts of the inflorescences. Mites too have sometimes been taken (see Appendix II).

#### VI.7.4.4. Hanging bells

*Cassiope tetragona* is the only flower at Hazen Camp fitting this category. Büdel (1959a) postulates that similar hanging bells of *Galanthus* and *Leucoium* (Snowdrops) become warm by trapping warm air rising from the ground and reports elevations of as much as 11 C in sunny weather (Büdel, 1959a). This explanation seems apt for *Cassiope tetragona* as it is unlikely much greenhouse effect within the flower could be derived from heating of the small reproductive organs.

Field data of 17.VII.1968 under optimal conditions at a mean ambient temperature of 16.3 C showed the mean elevation above ambient in 14 flowers to be 3.7 C, making them a warm 20.0 C within. Other attempts to measure the temperature elevation were made with much the same, if not so high, results. On 22.VII.1967 under optimal conditions and mean ambient temperature of 8.0 C a mean elevation of 0.9 C was obtained for 12 flowers, and on 30.VI.1967 with a breeze the elevation within the corollas was 0.5 C for 8 flowers at a mean ambient temperature of 12.0 C (see Appendix III-5).

#### Insects

No insects were found within the bells of these flowers despite extensive hunting in the hope of finding some indication of a relationship such as is described by Hagerup (1950).

#### VI.7.4.5. Discs

The composites make up the disc flowers at Hazen Camp. Those examined



were *Taraxacum arctogenum*, *Arnica alpine*, and *Erigeron compositus*.

VI.7.4.5.1. *Taraxacum arctogenum*

Büdel (1959a, b) measured the temperature within dandelion flowers under sunny conditions (as well as others) and found that they could be as much as 10 C hotter than the ambient air. Under the less intense arctic sunshine Shamurin (1966b) found temperature elevations in *Taraxacum macilentum* Dahlst. from 2.4 to 3.4 C.

A simulated 24 hours of sunshine was given to four inflorescences on 28.VII.1966 (Appendix III-6-1). The results, presented in Fig. 39 closely follow the expected sine or cosine law. A second experiment done on one head on 17.VII.1967 showed much the same results, but they were marred due to the passage of some thin high altocirrus clouds which partially obscured the sun (Appendix III-6-2). The maximum temperature obtained when the inflorescences were normal to the sun's rays was 5 C.

These results make good qualitative comparisons for curve shapes resulting from similar experiments on parabolic or bowl shaped flowers. The sine curve should be kept in mind henceforth.

In the field the temperatures of *Taraxacum* flowers conformed with the experimental data. On 7.VII.1968 two readings were taken from each of five flowers under optimal conditions at a mean ambient temperature of 20.5 C and an elevated mean temperature of 3.5 C was found. Similarly, on 2.VII.1968 at a mean ambient temperature of 9.5 C in the very early morning (weak sun) a mean elevation of 2.0 C was measured from 18 heads (Appendices III-6-3 and 4).

In cloud the temperature elevation disappears, for five inflorescences it was only 0.2 C.

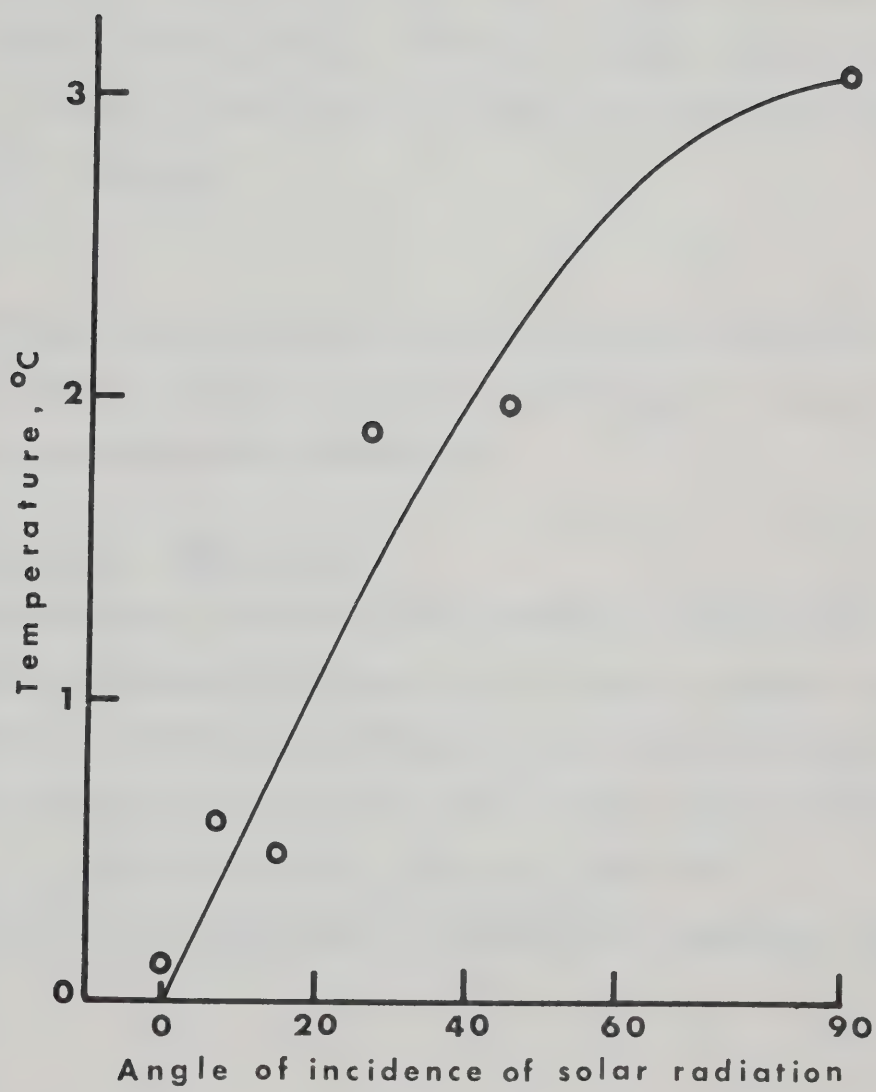






Figure 39.

Mean temperature excesses (C above mean ambient) of inflorescences of *Taraxacum arctogenum* with respect to the angle of solar incidence under optimal conditions (open circles), compared with theoretical (sine) curve (line).





## Heliotropism

The flowering heads of this species may be somewhat heliotrophic, that is they may follow the sun, provided that it is shining, for some part of the day. The habit of these plants of growing on banks, and their relative scarcity, make it difficult to obtain adequate data to present a detailed account such as is found for *Dryas integrifolia* and *Papaver radicum*.

## Insects

Although a great diversity of insects was seen from time to time visiting the inflorescences, none was seen to alight for longer than necessary to drink nectar (Appendix II).

### VI.7.4.5.2. *Arnica alpina*

Inflorescences of this plant were mounted at the same time on 17.VII.1967 as *Taraxacum arctogenum* and the results (Appendix III-6-5) show the same effect of shading due to the thin alto-cirrus cloud. The mean temperature elevation was 4.9 C at a mean ambient temperature of 17.5 C; a value very close to that of *T. arctogenum*.

During overcast conditions the inflorescence temperature falls to ambient.

## Insects

At Gilman Camp, where the above experiment was performed, *Arnica alpina* grows in considerable abundance. All the butterflies were seen to take up thermoregulatory postures on insolated inflorescences, moths, empidids, tachinids, muscids, culicids, calliphorids, chironomids, and the crab-spider, *Xysticus deichmanni* were frequently seen resting on them



for extended periods of time (see Appendix II) no doubt becoming considerably warmed by the sun and the inflorescences.

VI.7.4.5.3. *Erigeron compositus*

In the field temperatures within the inflorescences of this plant were taken on 7.VII.1968 under optimal conditions at a mean ambient temperature of 18.0 C. The mean elevated temperature within 10 inflorescences was 6.2 C for 20 readings. On 5.VII.1968 a mean temperature elevation of 3.0 was found for 10 flowers (3 measurements each) but there was a wind of 4 mps at the time. (Appendices III-6-6 and 7).

The only species of insect found consistently within the inflorescences is the agromyzid, *Phytomyza erigerontophaga*. The activities of these flies are obscure, however, they have been seen mating, and possibly feeding on nectar on occasional instances (Appendix II).

VI.7.4.5.4. Other discs

These are *E.eriocephalus* and *Chrysanthemum integrifolium* and are probably similar to the above. They are not often visited by insects.

VI.7.4.6. Parabolic or bowl-shaped flowers

The term parabolic flowers is not entirely correct. The flowers considered here are bowl shaped and may be approximated to spheric sections or something between these and paraboloids. Such flowers were examined by Büdel (1959a, b) (*Crocus*, *Eranthis*, and Tulip) and he assumed the elevated temperatures within these flowers in the sunshine to be due to conduction after radiative warming direct from the sun. Hocking and Sharplin (1965) attributed the effect in *Dryas integrifolia* and *Papaver radicatum* to the parabolic shape and reflecting properties





of these flowers, which would focus the heat on the sporophylls. They measured increments of about 3.6 C (6.5 F) and about 5.9 C (10.5 F) at the focus of *D. integrifolia* and *P. radicum* respectively, and found that this effect decreased noticeably away from the principle focus of the flowers. The above was noted in conjunction with flower basking in both sexes of both species of *Aedes* at Hazen Camp. They also noted that the flowers they studied turn with the sun throughout the 24 hours. A brief discussion of this is necessary before proceeding.

VI.7.4.6.1. Heliotropism\* in some arctic flowers

Although such inflorescences as *Helianthus\*\** and other flowers have long been known to face the sun (Hooker, 1881; Wiesner, 1879, 1882) I can find no modern reference to this phenomenon. Leopold (1964) discusses briefly responses to the sun in plants, particularly leaves, but does not mention flowers or other inflorescences.

At various times during several days of sunny weather in 1967 and 1968 about 1,300 flowers of *Dryas integrifolia* and 137 flowers of *Papaver radicum* were counted and the direction their radial axes made with respect to the sun (horizontal component only) noted correct to 45°. The results of this work are given in Table 28 and plotted in Fig. 40.

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\* Heliotropism is used here to describe the epinastic response of plants directly to the sun. Loeb (1890) used the term to describe what is now known as phototaxis (Fraekel and Gunn, 1960) and early botanists used the term to designate what is now called phototropism. Here Heliotropism is used as a division of phototropism to describe turning to the sun, as is suggested by the etymological derivation of the term from Greek.

\*\* The French for sunflower is *tournesol*, meaning turning to the sun.







Looking at the data from *Dryas integrifolia*, it can be seen that the heliotropic period starts at about 04:00 solar time and ends at about 17:00, a span of 13 hours, during 9 of which more than 50% of the flowers are pointing directly at the sun, and during 7, more than 70% are so directed. At about 13:00 heliotropy diminishes as some flowers lag behind and are counted in the "315° to the sun" category. This group apparently stay behind in that position with respect to the plant clump, and so 3 hours later are counted in the 270° category. The lag in these two curves is clearly shown in Fig. 40. After this time, more lagging can be seen, particularly 225° and 180°, but these are obscured by the lagging of the remaining flowers and by the disarray of the flowers in a clump following the cessation of heliotropism with the weakening sun. Eventually, when one considers those pointing at 45° to the sun, that is just about as they are to resume heliotropism. The flowers show no particular orientation.

*Papaver radicatum* remains heliotropic throughout the 24 hours of sun. During 13 different times throughout the 24 hours all the flowers of this plant were found directly facing the sun (see Fig. 40).

Other flowers, not studied, which may be heliotropic to some extent are *Potentilla nivea* and *Taraxacum arctogenum*.

The significance of heliotropism is clear in relation to the microthermic environment within flowers facing the sun as compared with flowers not doing so. These flowers are heliotropic only during relatively calm weather, and when the sun is shining. Wind carries the flowers with it, and during cloudy conditions no particular orientation is noticeable. The heliotropism is not an endogenous circadian rhythm within these flowers, as is demonstrated by their lack of turning when







Figure 40.

Per cent of heliotropic flowers of *Dryas integrifolia* and *Papaver radicum* throughout a day (composite of several days observations).

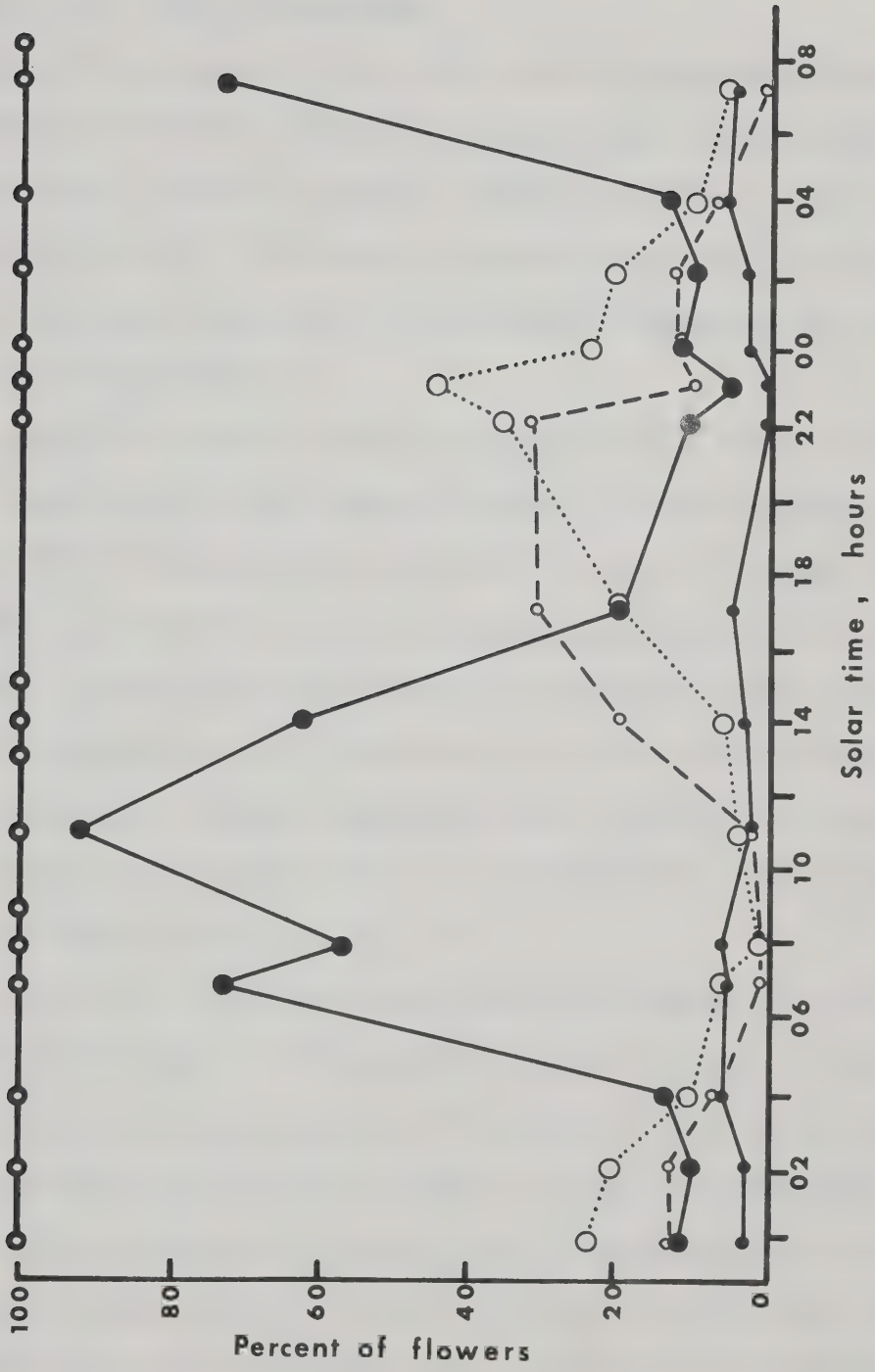
Heavy open circles and solid line, *P. radicum*.

Large solid circles and solid line, *D. integrifolia* facing directly to sun ( $0^{\circ}$ ).

Small solid circles and solid line, *D. integrifolia* at  $45^{\circ}$  to sun.

Small open circles and broken line, *D. integrifolia* at  $315^{\circ}$  to sun.

Large open circles and dotted line, *D. integrifolia* at  $270^{\circ}$  to sun.





the sun is obscure and the light diffused.

VI.7.4.6.2. *Dryas integrifolia*

During the seasons of 1966 and 1967 some 10 experiments were set up to measure the corolla temperatures of variously treated flowers over a simulated 24 hours of sunshine assuming the flower to be stationary (i.e. not heliotropic). Treatments involved normal flowers, decorollate flowers, and flowers from which the reproductive organs had been excised or desporophyllate flowers.

The results are given in detail in Appendix III-7 showing the mean elevated temperatures of the flowers according to their treatments together with the mean ambient temperatures for each. The data from 14.VII.1967 and 8.VII.1967 has been plotted comparatively in Fig. 41. This is the only data which are absolutely comparative as the experiments were done in conjunction with one another at the same time and under the same conditions. Ambient temperature has a profound effect on the extent to which the phenomena occur as is exemplified by the inclusion of the data from 26.VII.1966 in Fig. 41.

From Fig. 41 it can be seen that the flower comprised of the corolla alone with their petals in the paraboloid form are capable of warming thermocouples held at the position of the excised stigmas to the same extent as when the whole flower is intact. As this desporophyllate flower is tilted through the simulated day its temperature at the principle focus drops off more rapidly than that of the entire flower, and also faster than that of the decorollate one. The curve for the decorollate flower, in fact, falls off slightly less rapidly than that of the intact.

This is explained because the decorollate flower can be regarded



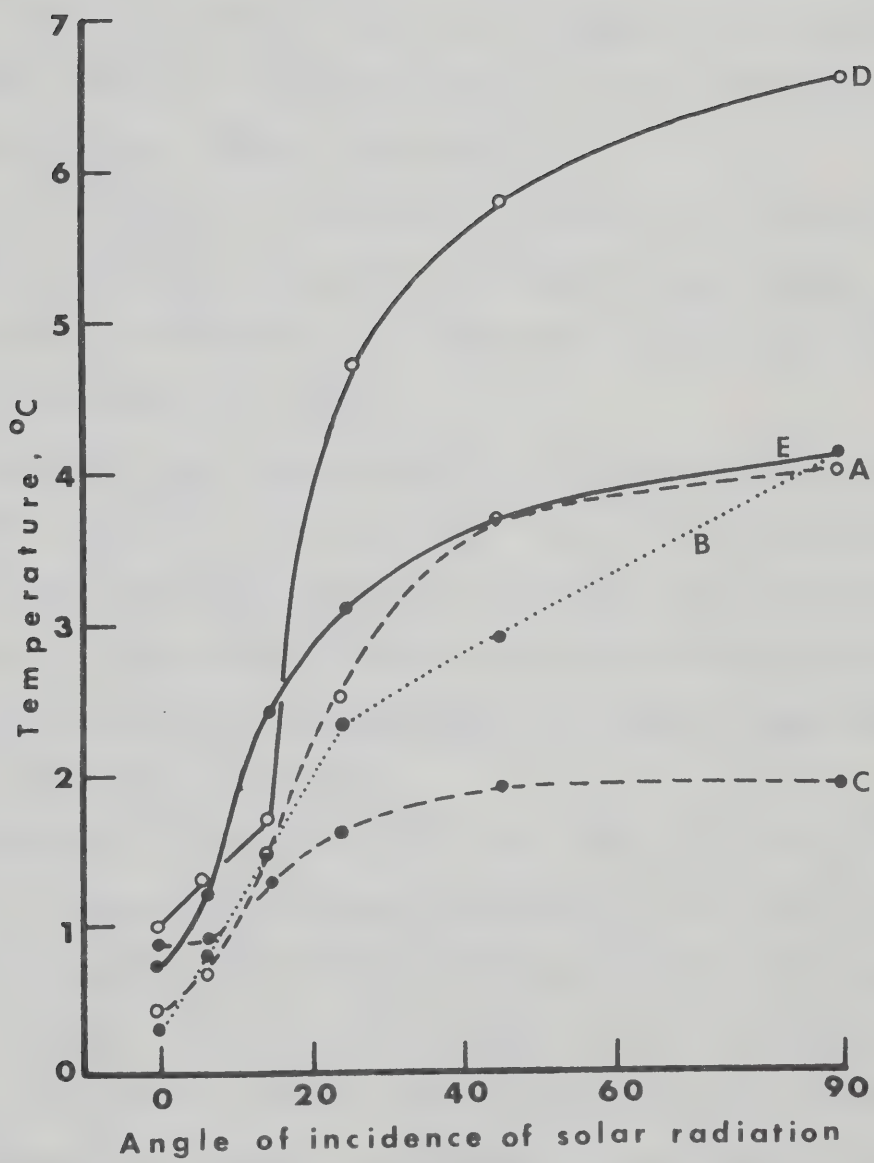


Figure 41.

Mean temperature excesses ( $^{\circ}$  C) in flowers of *D. integrifolia*  
A-C, 8.VII.1967; D-E, 26.VII.1966.

A	Entire flowers	Appendix III-7-2
B	Desporophyllate flowers	Appendix III-8-10
C	Decorollate flowers	Appendix III-7-7
D	Entire flowers	Appendix III-7-3
E	Decorollate flowers	Appendix III-7-6







as roughly hemispherical and absorbs energy from the sun equally at almost all angles above about  $26.5^{\circ}$ . Below this value the amount of surface area presented to the sun falls off, and so similarly, the temperature. The effect of the internal parts, sporophylls, is seen in the slow rate of fall in the intact flower, which can be regarded as the superposition of the steep decline in the desporophyllate and the slow decline in the decorollate flowers; giving curves A and D.

It is interesting that the effect of shading by the petals, reducing the parabolic focussing drastically, and hence the temperature; and the sharp decline of temperature in the decorollate flowers occur more or less at the same angle (ca.  $26.5^{\circ}$ ).

An important point about the three curves describing the above is the relative positions of the end points. The curves for the normal and desporophyllate flowers reach the same maximum values together, while the curves for normal and decorollate flowers share the same minimum value, while the curve for the desporophyllate flowers plunges well below the other two at its minimum.

To summarize: it seems that the corolla acts as a reflector, parabolic or spherical, which when directed exactly into the sun focusses heat on the principle focus at the approximate position of the stigmas. It does so whether the sporophylls are there or not. However, as the flower is tipped out of normal to the sun's rays the focussing effect becomes lessened by diffusion or astigmatism or both (curve B) while the convective warming from the sporophylls (as per curves C and E) hinders the lessening of the former effect thereby giving the resultant effect noted in curves A and D, that of the normal intact flower.

With this in mind it is easy to understand the selective advantage



of heliotropism particularly by paraboloid flowers in the arctic where the heat budget is low and warmth at a premium.

#### Field data

Field results taken at different times of the day and on a number of occasions during the three seasons are different but fit well within the experimentally obtained figures obtained for flowers pointing at the sun. On 5.VII.1967 for example, under optimal conditions when the mean ambient temperature was 7.5 C, the mean elevated temperature taken within 12 normal flowers was 5.6 C, and 4.4 C in 8 desporophyllate flowers (Appendix III-7-11 and 12). Again on 7.VII.1968 when the mean ambient temperature was 15.0 C the mean temperature elevation for 10 flowers and 52 readings was 7.3 C using intact flowers (Appendix III-7-13 and 14). The temperatures in normal heliotropic flowers usually lie between 3 C and 10 C above the ambient air temperature on sunny days.

As can be seen from the heliotropism curve (Fig. 40) not all the flowers are directed to the sun. The effect of aspect was therefore examined using 80 flowers under optimal conditions at a mean ambient air temperature of 8.8 C, on 5.VII.1968 (Appendix III-7-15). The results which one would expect were indeed observed. The heliotropic flowers were 3.2 C above ambient, while those facing away from the sun were at 1.1 C, and those at right angles lay in between (Fig. 42). These values are somewhat lower than might be expected due to a slight breeze but nevertheless differ significantly according to aspect. On 7.VII.1968 temperatures within heliotropic versus reversed flowers were measured and the results fit the above pattern (Appendix III-7-14).

Many readings were taken to determine whether or not the intact

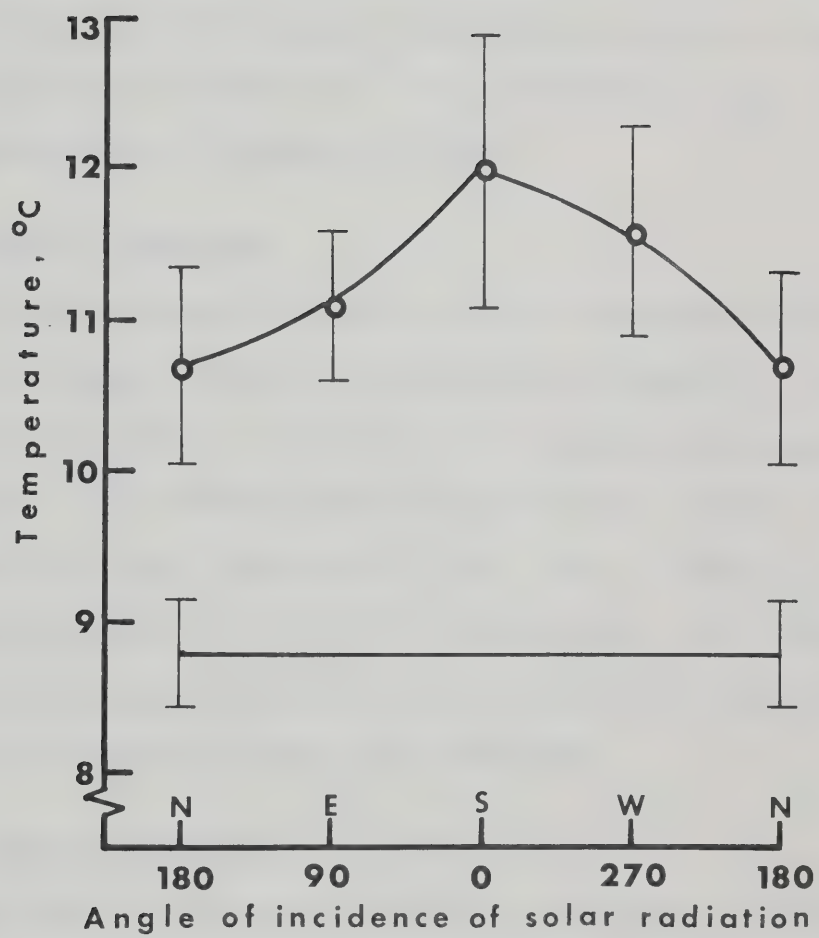






Figure 42.

Temperatures in *D. integrifolia* flowers around a clump at different angles of incidence of solar radiation (S facing sun, N away from sun) at Hazen Camp, 5.VII.1968.  
Horizontal line, mean ambient air temperature; vertical lines, one standard deviation either side of the mean. (Appendix III-7-15)





flowers are warmer deep among the sporophylls than at the stigmas. The results show that there is little or no difference. In general the flowers are between 0.5 and 1.0 C warmer amongst the sporophylls, but on occasion were 0.5 C cooler.

During heavy overcast conditions the temperature of *D. integrifolia* flowers drops to that of the ambient air, just as it does in shade. Variation may be plus or minus 0.5 C. On 16.VII.1967 the mean elevation for 30 flowers was 0.2 C (Appendix III-7-16).

#### Effect of ambient temperature

These data were obtained through combining experimental and field results for the range of mean ambient temperatures available. These range from 4.0 C to 15.0 C, while the corolla temperatures range from 7.3 C to 22.5 C. The scatter diagram (Fig. 43) shows a linear relation with a slope of 0.75 and a formula of  $0.75X - 1.92 = Y$ , where X is the corolla temperature and Y is the ambient temperature. This formula is derived from the data described above and does not take into consideration time of day or intensity of direct solar radiation.

#### Effect of radiation intensity

Although there is undoubtedly an effect of decreased solar intensity correlated with the sun's angle of elevation and thus the time of day, on corolla temperatures it was impossible to measure. The effects of changes in the ambient temperature certainly masked them, and they are probably incorporated into Fig. 43.

#### Effect of wind

On 28.VI.1967 an experiment was set up in optimal conditions. Shortly

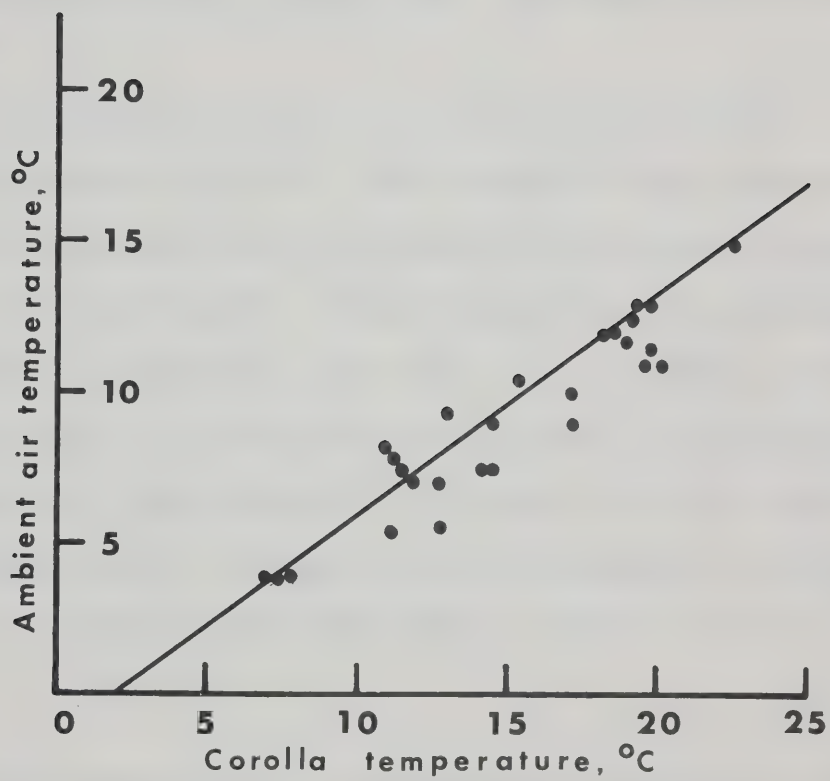




Figure 43.

Effect of ambient temperature on corolla temperature of *D. integrifolia*.







afterwards a breeze got up and continued to strengthen from calm to 3 mps. During this time corolla temperatures were measured when the corolla was exposed to the wind (W) and when it was sheltered from it (S). At the same time as the ambient temperature (A) was taken. With this information it is possible to simply calculate the proportion of the corolla temperature remaining at different wind speeds (Q) according to the following formula  $Q = (W-A)/(S-A)$ . The values of Q are plotted in Fig. 44.

With the information in Fig. 43 it was possible to verify, to some extent, the validity of Fig. 44. This was done by using field data of corolla temperatures taken while breezes were blowing at a measured velocity, and taking from Fig. 43 the 'expected' corolla temperature for the ambient temperature at that time, and so obtaining more values for Q. Both sets of Q values are reasonably close and lend strength to the validity of Figs. 43 and 44. The results are given separately in the combined Fig. 44. The curve can be approximated to a parabola of  $0.75Y^2 = X$ , where  $Y = \text{wind speed (mps)}/3.3 \text{ mps}$  and  $X = Q - 1$ .

#### In rain

During the summer of 1966 it rained several times, and on one occasion in 1968. Flowers standing upright became partially filled with water, while those bent over or blown by wind were dry. I noted some insects, particularly *Rhamphomyia* spp. remained within these dry flowers during rain. *Saxifraga oppositifolia* may also shelter insects from rain, but in a different way (see below).





Figure 44.

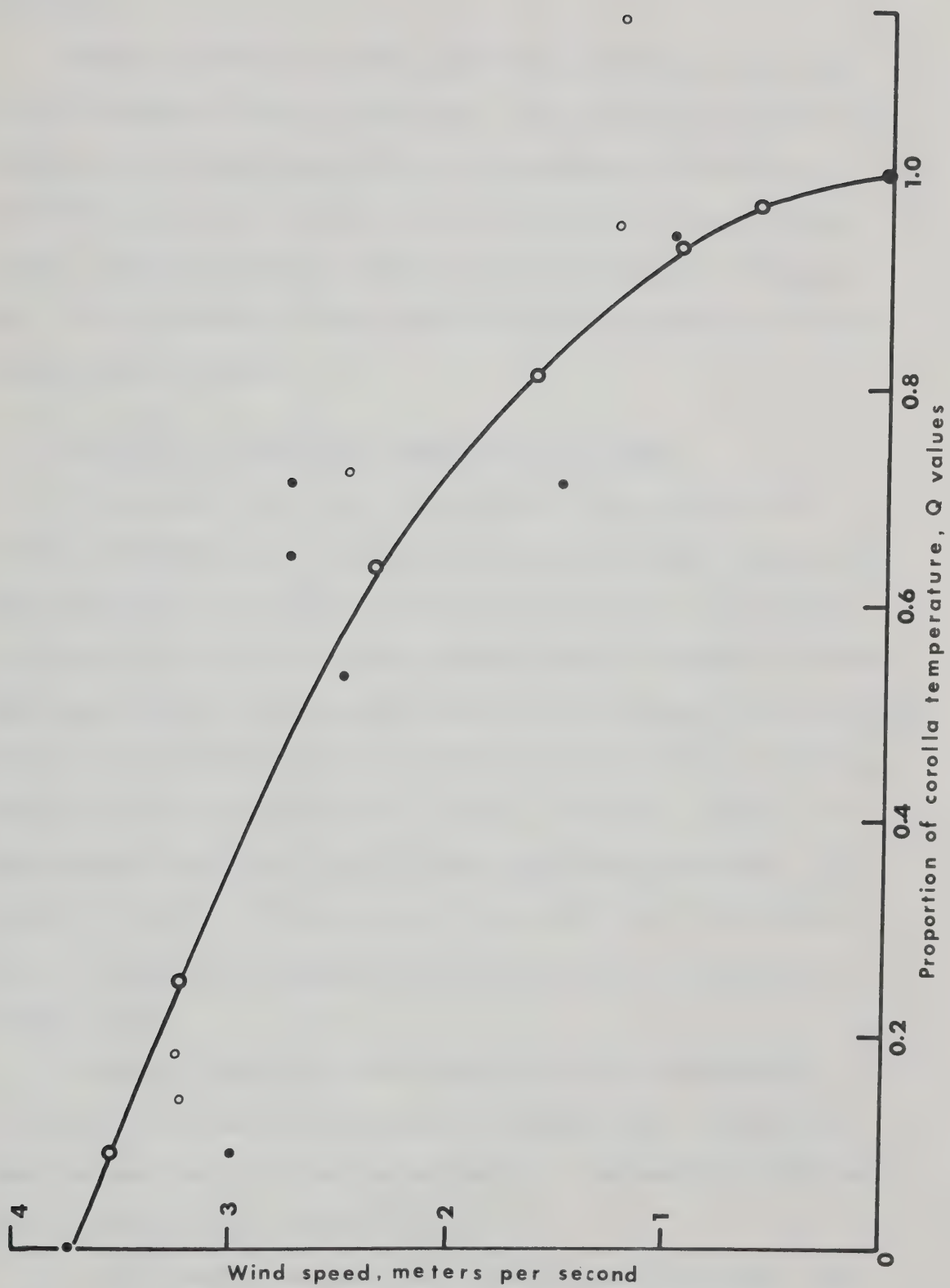
Reduction of corolla temperature in *D. integrifolia* with increasing wind.

solid circles -- results from 28.VI.1967.

open circles -- extrapolated from corolla temperatures taken at known wind speeds and ambient temperatures (using Fig. 43).

heavy open circles

-- parabola  $Q-1 = .75 \left( \frac{\text{wind speed, mps}}{3.3 \text{ mps}} \right)^2$







## Insects

Hocking and Sharplin (1965) noted flower basking by both sexes of both species of *Aedes* at Hazen Camp. Far more commonly found flower baskers are the Empididae, particularly *Rhamphomyia filicauda* and *R. nigrata*; *R. hoeli* is quite common between the sporophylls and petals. Among the muscids several species bask, notably *Spilogona* spp. Other observations were made on chironomid, syrphid, and lepidopteran flower baskers.

### VI.7.4.6.3. Insect body temperatures in flowers

To understand this flower basking habit and to discover its relative importance, the body temperatures of the larger insects were measured within and outside the flowers. The insects were impaled on a thermocouple, which had been inserted into the thorax from behind. The larger insects used responded well to this treatment, often actively siezing the sporophylls of the flower they were placed on; so holding themselves and the thermocouple in place. On several occasions the experimental animals were lost as they worked themselves free of the wires and flew off. Smaller insects (e.g. *Aedes* spp.) were killed by the treatment, but measurements were taken only as long as the insects lived.

On several occasions in 1967 and 1968 the body temperatures of a variety of insects were measured in flowers of *D. integrifolia* under optimal conditions and facing the sun. The results of this are given in Table 29 and Appendices IV-1 to 9.

It can be easily seen that the elevations are considerable and can be regarded as important contributions to the overall metabolism



Table 29.

Body temperature excesses of various insects in flowers of *D. integrifolia* at Hazen Camp.

Species	Appendix No.	Date	No. of insects	Mean ambient T (°C)	Mean body temp. excess (°C)		Range (C)	
							Max.	Min.
<i>Aedes nigripes</i>	IV-1	28.VI. 67	9	10.5	+ 5.9		6.5	5.0
<i>Aedes</i> spp.	IV-2	19.VII.67	2	16.0	+ 6.2		6.5	5.8
	IV-3	7.VII.68	4	12.1	+ 6.1		8.0	4.0
	IV-4	8.VII.68	24	14.2	+10.1		16.0	3.5
<i>R. filicauda</i>	IV-5	27.VI. 67	18	12.5	+ 6.2		9.5	4.5
<i>R. nigrita</i>	IV-6	8.VII.68	18	15.1	+12.0		16.5	8.0
<i>Carposcalis carinata</i>	IV-7	8.VII.68	4	13.4	+ 3.5		16.7	10.3
<i>Boreellus atriceps</i> *	IV-8	8.VII.68	4	17.5	+15.4		17.4	11.3

\* Not a flower basker



of the insects using flowers for heat.

Having already noted the importance of the petals in elevating the intrafloral temperature the next step examines their effect on the body temperatures of insects. Entire decorollate, and desporophyllate flowers were used and the body temperatures of various insects was taken in the three experimental types of flowers. The results are given in Table 30.

Table 30 shows that all the insects are warmer than the ambient air as a result of radiative solar heating; they are all between 3 C and 5 C significantly above ambient (Appendices IV-10 to 16). When perched on decorollate flowers their body temperatures are increased significantly (Appendices IV-10 to 16) as they absorb extra convective heat from their substrate, the sporophylls. Insects held in desporophyllate flowers at the height of the stigmas show a still more significant increase, amounting to 4 times that when in the air alone. Little further increase was noticed when these insects were placed in whole flowers, the increase being generally less than 1.0 C and insignificant (Appendices IV-10 to 16). These are the expected results considering Figure 41 and its explanation.

The temperature excesses in the insects within the intact flowers are considerably greater than the temperature excess of the flowers alone, as would be expected.

Differences in the extents to which this warming occurs are to be expected on the basis of the sizes, colours and shapes of the insects used (see Digby, 1955). The posture of the insects too must have an effect; *Aedes* spp. with their long legs tend to stand higher off the sporophylls than the other insects considered. The results fall into





Table 30.

Insect body temperature excesses in entire, decorollate, and desporophyllate flowers of *D. integrifolia*.

<u>Species</u>		<u>Date</u>	<u>No. of insects</u>	<u>Mean ambient T (°C)</u>	<u>Entire</u>	<u>Desporophyllate</u>	<u>De-corollate</u>	<u>Air</u>
<i>Aedes</i> sp.	IV- 9	19.VII.67	2	16.0	+ 5.8	+ 6.5	+ 4.0	+4.0
	-10	28.VI. 67	4	10.5	+ 5.8	--	--	+4.1
	-11	7.VII.68	2	12.1	+ 4.5	+ 4.5	+ 2.2	--
	-12	8.VII.68	10	13.9	+12.9	+11.6	+ 6.4	+3.4
<i>R. filicauda</i>	-13	27.VI. 67	5	13.0	+ 6.0	--	--	+4.8
<i>R. nigrita</i>	-14	8.VII.68	10	15.0	+14.0	+13.8	+ 9.7	+4.8
<i>Carposcalis</i> <i>carinata</i>	-15	8.VII.68	4	13.4	+15.3	+15.0	+10.7	+5.1
Calliphorid <i>B. atriceps</i>	-16	8.VII.68	3	17.5	+15.4	+15.0	+10.7	+3.3



the pattern presented by Digby (1955). These field data do not lend themselves to rigorous treatment.

Simulated 24 hours of sunlight experiments were set up with insects in *D. integrifolia* flowers to determine the effect of the solar angle of incidence on the body temperature excess of flower basking insects.

I experimented on 5 specimens of *Rhamphomyia filicauda* under optimal conditions at a mean ambient temperature of 12.8 C (27.VI.1967). The data (Fig. 45, Appendix IV-17) show that in intact flowers the insects' body temperatures fall off slightly faster with decreasing angle of insolation than would be expected within the flower alone (see also Fig. 41). The reason for this is not clear; it may be due to experimental variation. Further along the curve towards the origin the cooling of the insect proceeds more slowly with decreasing solar angle than it might be expected to in the intact flower. This is because the insect above the flower is absorbing solar radiation, as well as absorbing the remains of the heat from the flower. *R. filicauda* rests directly across insolated flowers so that its long axis is horizontal, i.e. normal to the axis of solar rotation about the flower. Thus these insects can be likened to cylinders which will cool according to the sine law as the sun moves around their flowers. This whole complex of curves is presented as one in the results given by curve 1 in Fig. 45 and Appendix IV-17.

On 28.VII.1967, 2 specimens of *Aedes nigripes* were treated as above, and 2 others on 19.VII.1967 similarly but in three experimental types of flowers, normal or intact, desporophyllate, and decorollate when the mean ambient temperature was 16.0 C. The data are presented in Fig. 45. Starting with curve 4, which shows the relationship





Figure 45.

Body temperature excesses of insects in flowers of *Dryas integrifolia* with respect to angle of incidence of solar radiation, Gilman Camp, 1968.

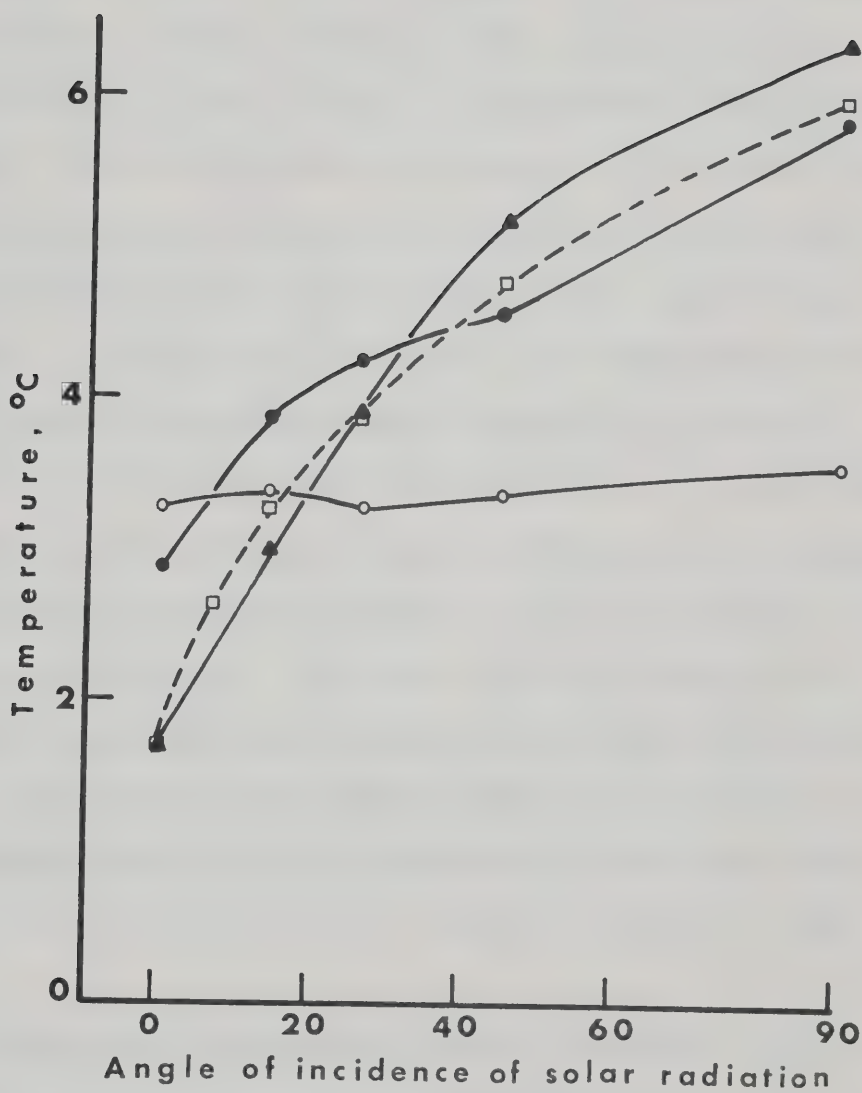
Solid lines    *Aedes* sp.

solid circles, in entire flowers

open circles, in decorollate flower

solid triangle, in desporophyllate flower

Broken line    *Rhamphomyia filicauda* in entire flowers







between solar angle of incidence and the insects' body temperatures, one can see a straight line parallel to the X axis at a temperature of about 3.5 C. Mosquitoes sit in the flowers vertically, or parallel to the axis of rotation of the sun through their flowers. Likening the mosquito to a cylinder oriented as above one can see that no matter the angle of solar incidence, an equal amount of radiation will be absorbed. This is precisely what is seen. This accounts for the body temperatures of mosquitoes not dropping as low as those of the *R. filicauda* specimens in the normal flower: compare curves 1 and 2. Also it accounts for the curves 1 and 4 being almost equal at the Y intercept (sun shining across the top of the flowers). Curve 3 for the desporophyllate flowers with *Aedes* sp. within drops below curves 2 and 4 because at those low angles of solar incidence the insects were essentially suspended in the open air and not receiving heat from the sporophylls. This drop, with that probably due to difficulties in correct posturing and shading effects, account for the total drop, which may be somewhat larger than it should be. This curve resembles that of Fig. 41, indicating the mosquitoes' body temperatures are following the flowers' temperature, which is quite likely.

The behavioural significance of posture differences from one species of basking insects to another is unclear.

Warming and cooling rates of insects in *Dryas integrifolia* flowers.

The reason for determining warming and cooling rates on insects visiting and basking in flowers is twofold. Firstly, to determine how soon after landing in a heated corolla are insects heated to



maximum, and secondly, to determine whether the insects have any powers of thermoregulation through muscular action to slow cooling.

The temperatures of the insects was taken after 10 or 15 second intervals after exposure to or shading from the sun. The experiments were conducted on insects placed in flowers. *Dryas integrifolia* itself takes some 50-60 seconds to warm and cool (5 observations on each at 4 C under optimal conditions, 8.VII.1967 and a similar 5 on 14.VII. 1967 at 9 C).

Differences between species follow the size of the insect, the larger it is the longer it takes to reach an equilibrium. Figs. 46 and 47 show warming and cooling rates for those insects studied. These curves compare favourably with similar results presented by Digby (1955).

It is apparent that insects can very quickly make use of the solar energy to warm themselves, and do so very well within the corollas of flowers such as *Dryas integrifolia*, responding within a matter of seconds to maximum. They do not regulate their body temperatures through any metabolic processes or muscular activity, such as is known for many insects, particularly moths and bees (Wigglesworth, 1965).

Differences in the warming and cooling curves between species is easily explained according to differences in size and shape. As the surface to volume ratio decreases the slower becomes the temperature change, and the longer it takes for the insects' body temperature to reach equilibrium. The surface to volume ratio decreases with size and with compactness. This is shown when comparing the thin small mosquitoes with the squat large blow-flies. Other differences





Figure 46.

Cooling rates of insects in flowers of *Dryas integrifolia*, Gilman Camp, 1968.

Open squares, *Boreellus atriceps*

Solid squares, *Carposcalis carinata*

Open circles, *Rhamphomyia nigrata*

Solid circles, *R. filicauda*

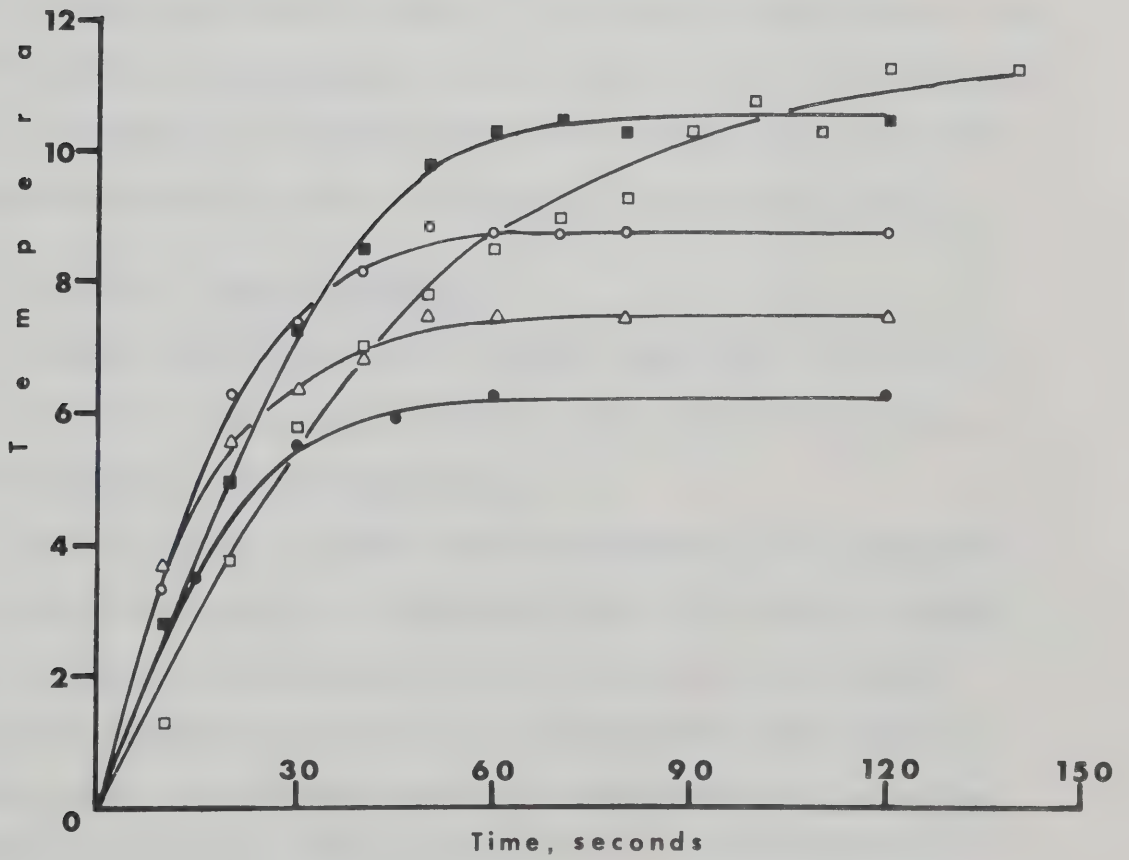
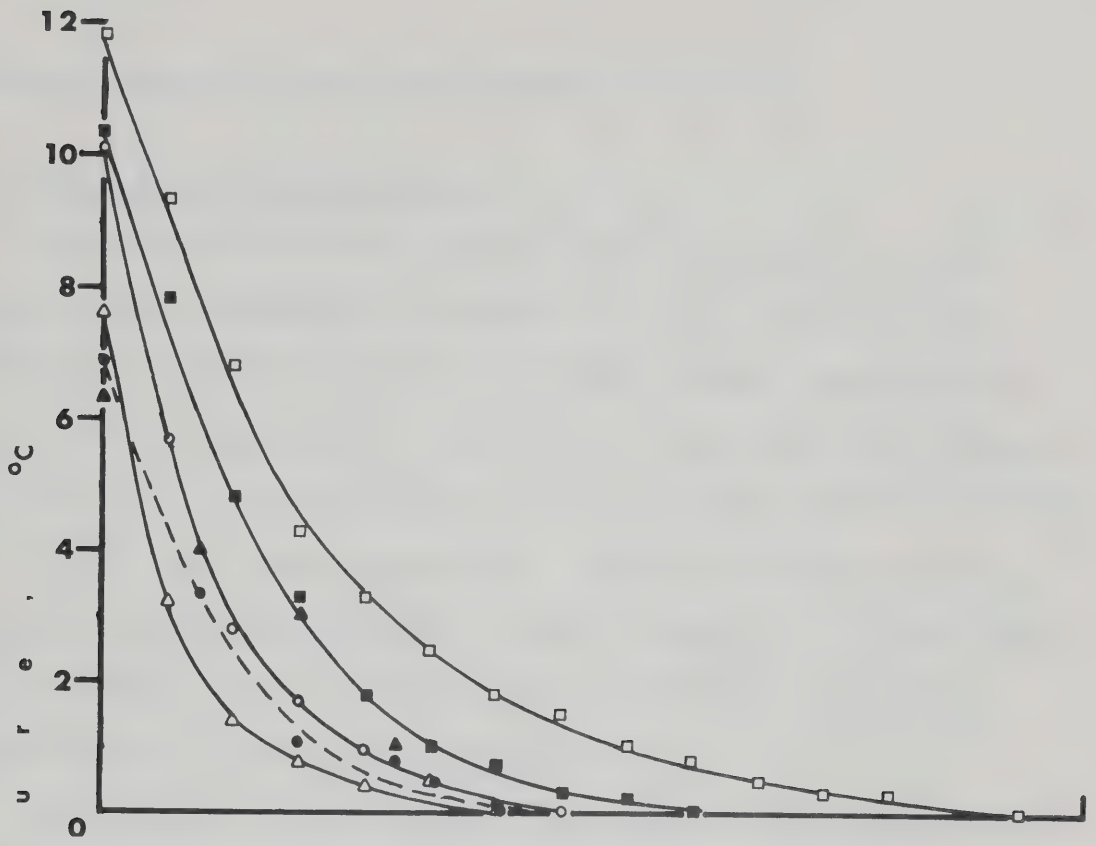
Open triangles, *Aedes* sp. (female)

Solid triangles, *Aedes nigripes* (females)

Figure 47.

Warming rates of insects in flowers of *Dryas integrifolia*, Gilman Camp, 1968. (Legend as in Fig. 46)







can be attributed to colour and hairiness differences.

VI.7.4.6.3. *Potentilla nivea*

*Potentilla nivea* is the smallest bowl shaped flower. It was experimented on throughout a simulated 24 hours of sunlight on two occasions, 17.VII.1967 and 28.VII.1966 under optimal conditions and at a mean ambient temperature of about 17.5 C. The results (see Appendix III-7-18 to 20) are qualitatively similar to those of *Dryas integrifolia*.

In the field these flowers show a temperature excess comparable to those obtained experimentally. A mean elevation of 2.8 C was noted for 30 readings taken at a mean ambient temperature of 9.0 C for flowers facing into the sun (Appendix III-7-21).

These flowers are not noticeably heliotropic. In shade the intra-floral temperature drops to ambient. Few insects were collected from these flowers. Most were empidids and syrphids, also found frequently on *D. integrifolia*. Shamurin (pers. comm.) noted flies resting for extended periods in flowers of *Potentilla* in the Soviet arctic.

VI.7.4.6.4. *Papaver radicatum*

Hocking and Sharplin (1965) recorded temperature elevations of up to 5.8 C in these parabolic flowers, and found that they have a definite focus, and are heliotropic.

On 28.VII.1966, 7 flowers were experimented on over a simulated 24 hours of sunlight for a stationary flower. The results resemble very closely those obtained for *Dryas integrifolia*, but are not absolutely comparative because of the differences in the ambient temperatures. The maximum elevation obtained was 7 C at an ambient temperature of 7.0 C. The data are presented in Appendix III-7-22



and Fig. 48.

Field observations taken on 7.VII.1968 showed that the above effect occurred naturally when 12 flowers proved to have a mean elevated temperature of 7 C, and up to 10 C at a mean ambient temperature of 16.1 C under optimal conditions (see Appendix III-7-23).

During overcast weather (e.g. 16.VII.1966 and 28.VI.1968) the corolla temperatures are almost the same as the ambient air (Appendix III-7-24, 25).

Poppy is not a very entomophilous flower. Various insects were taken from within its corollas, some (a few chironomids, empidids, and muscids) apparently basking. No insects were found consistently within the corollas. Although Hocking and Sharplin (1965) report on mosquitoes, Hocking (1968) does not mention them.

#### VI.7.4.7. Inverted Bells

Inverted bells are considered apart from the parabolic or bowl shaped flowers. This class of flowers resembles the traditional bell with its flared mouth. Flowers in this class do not hang as in the 'hanging bell' class, but rather are open horizontally to vertically upward.

##### VI.7.4.7.1. *Saxifraga oppositifolia*

On 21.VI.1966, simulated 24 hours of sunshine were directed on 10 intact flowers, and later on the same day in a comparative experiment on 5 intact flowers, 5 decorollate flowers, and 5 desporophyllate flowers. At this time measurements were made at the position between the two stigmas. The results of these two experiments are presented in Fig. 49 and Appendix III-8-1 to 4.

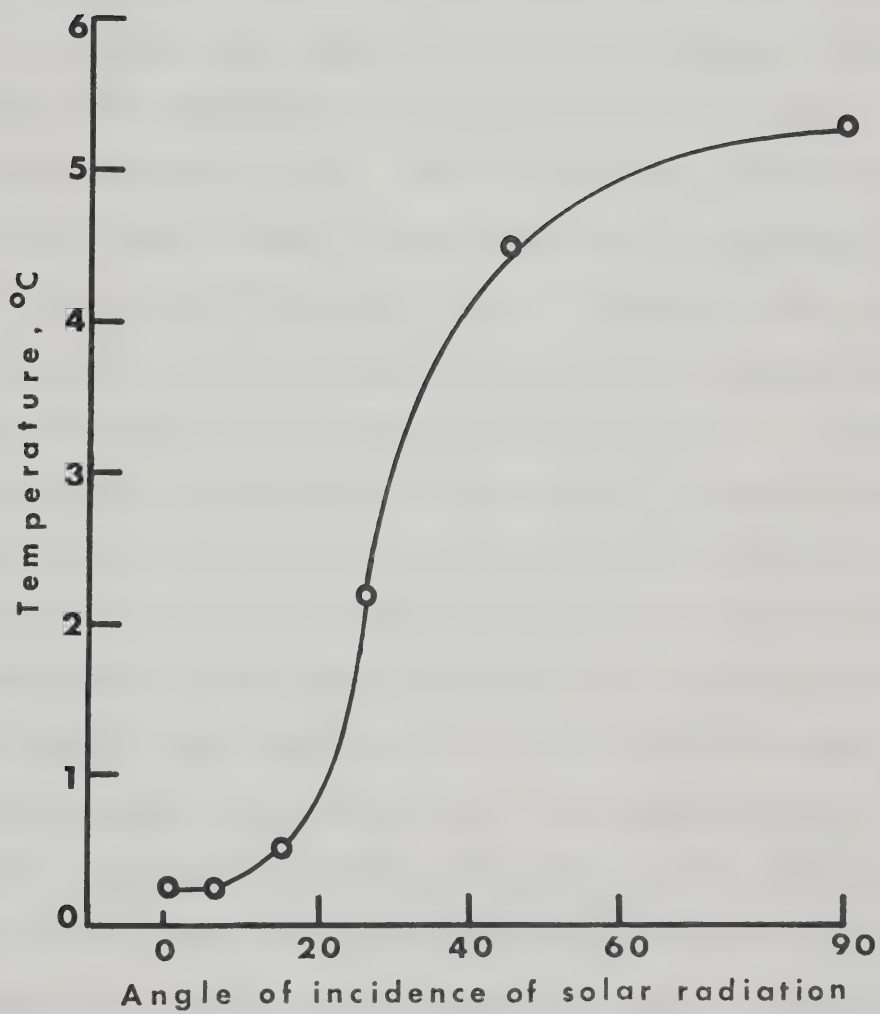






Figure 48.

Temperature excesses in flowers of *Papaver radicatum* with respect to the angle of incidence of solar radiation. Experimental observations, Hazen Camp, 1966.





Curve A (Fig. 49) shows a clear drop in temperature with decreasing solar angle of incidence; it is almost identical in shape with curve B in the second experiment although the figures are lower. Comparing curves B, C, and D the effect of the petals on the temperature and heating of the flowers is obvious. Curve D shows that there is some warming in the decorollate flowers, but only to the extent of 0.2 C; this is very little compared with curve C, showing an elevation of 1.2 C in the desporophyllate flower; and less still compared with curve B, 1.4 C in the intact flower. These curves can be compared with those for *Dryas integrifolia* given in Fig. 41 showing the same effects.

The majority of insects staying in the corolla are small chironomids, and rest at the bottom of the flower. Thus on 7.VI.1967, a simulated 24 hours of sunshine experiment was performed on 17 flowers in which the temperature was measured just above the base of the corolla inside. Conditions were optimal with a mean ambient temperature of only 2.0 C. The mean maximum value obtained with the flowers normal to the sun's rays showed a mean elevation quite close to that of curve A. The data are presented as curve E in Fig. 49 (Appendix III-8-5). Curve E shows considerable departure from curve A as the effect of shading within the corolla comes into play when the solar angle of incidence falls to about 45°, and the internal temperature drops off rapidly as this angle is further decreased and radiative losses from non-insolated flower parts increase. Unfortunately weather did not permit me to repeat this experiment.

In overcast weather or in shade, the temperature of these flowers drops almost to that of the ambient air, for example, on 16.VI.1966, the mean elevation for 10 flowers was only 0.1 C (Appendix III-8-6).





Figure 49.

Temperature excesses in flowers of *Saxifraga oppositifolia* with respect to the angle of incidence of solar radiation. Experimental observations, Hazen Camp, 1966, 1967.

Curve A at level of stigmas in whole flowers.

Curve B at level of stigmas in whole flowers.

Curve C at level of stigmas in desporophyllate flowers.

Curve D at level of stigmas in decorollate flowers.

Curve E at bottom of corolla in whole flowers.



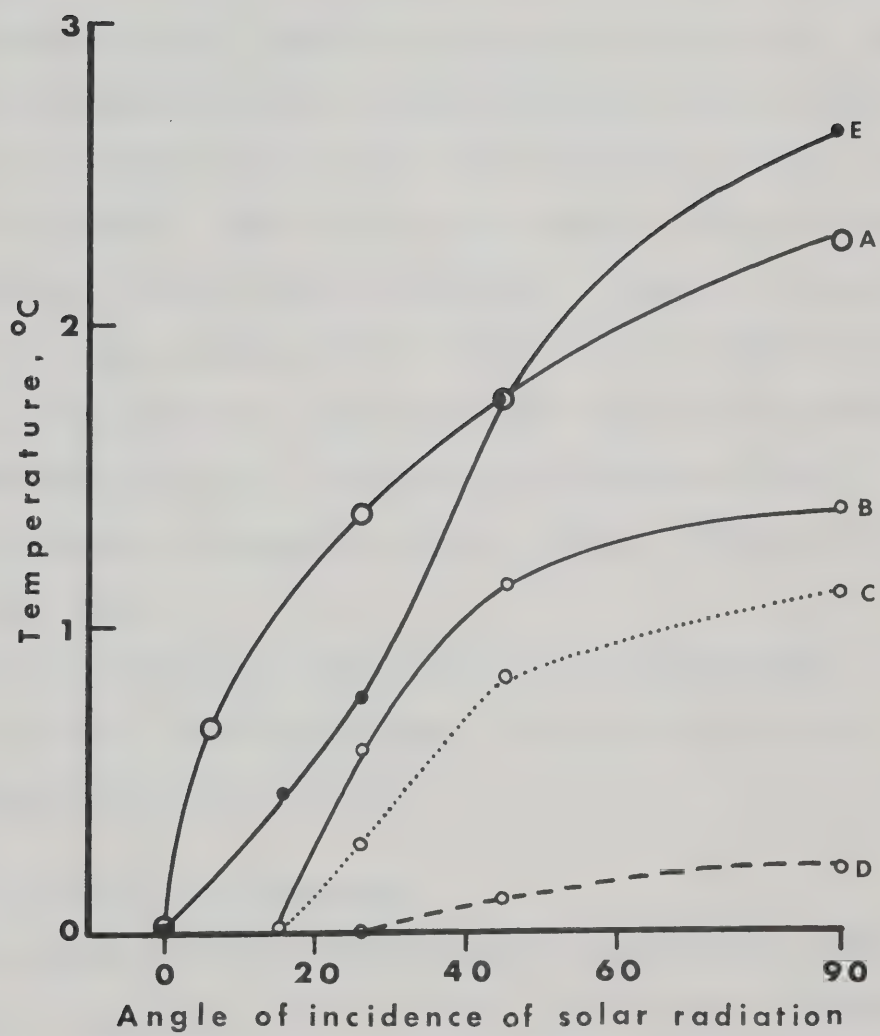
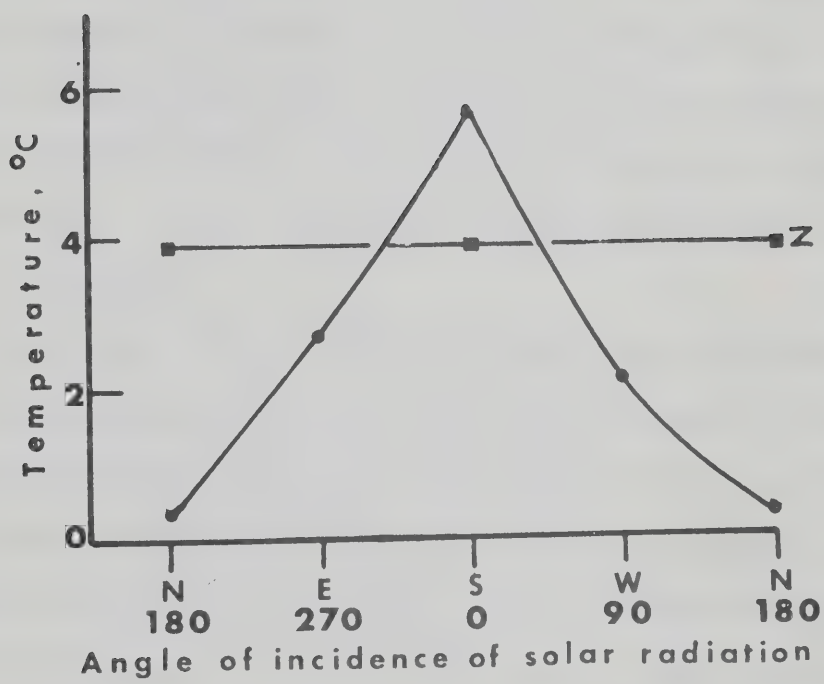






Figure 50.

Temperature excesses in flowers of *Saxifraga oppositifolia* with respect to the angle of incidence of solar radiation. Field observations, Hazen Camp, 1968. Squares, flowers orientated vertically; circles, flowers orientated horizontally.





of flowers and divided them into insolated and shaded halves. The chironomids were counted in each half at times throughout the day on a number of occasions in 1966 and 1968. The data are presented in Table 31. It shows that at all times of the day from 56.0 to 72.8% of the chironomids are in the insolated flowers. The probability of this occurring by chance is less than 0.001. For this to happen, the insects must be moving continually and finding warmer flowers. Whether they find the warmer flowers purely because of the extra warmth, or because of an indirect effect of the heat on the flower (e.g. greater scent) is not known. Almost certainly, orthokinesis (Fraenkel and Gunn, 1960) is involved.

In the rain (e.g. 22-24.VI.1966) these chironomids hide under the corollas of *Saxifraga oppositifolia*, using them as umbrellas. After 1 hour of rain on 22.VI.1966, 65% of these insects had already found their way under the flowers, 13 hours later this had increased to 79.5%. After the rain ceased the insects slowly resumed their positions in flowers so that after 14 hours of sunny weather, 89% of the chironomids were in the corollas.

#### VI.7.4.7.2. *Lesquerella arctica*

Under optimal conditions on 2.VII.1968 the temperature mean within 52 flowers was measured to be 1.4 C above the ambient temperature of 8.2 C (Appendix III-8-8). Similar results were obtained from 20 flowers on 7.VII.1968 when the corolla temperature elevation was 1.5 C at a mean ambient temperature of 18.4 C. During overcast conditions there is no temperature elevation and these flowers show slight closing.

The only insects found exclusively and with any consistancy in





Table 31.

Distribution of chironomids on clumps of *Saxifraga oppositifolia* flowers according to solar incidence and time of day at Hazen Camp.

<u>Time (EST)</u>	<u>Date</u>	<u>Insolated</u>	<u>Shaded</u>	<u>Total</u>	<u>% on insolated</u>
00:00	21.VI.1968	32	19	51	62.7
01:00	25.VI.1966	72	27	99	72.8
02:00	21.VI.1968	69	31	100	69.0
03:00	21.VI.1968	28	19	47	59.6
04:00		56	43	99	56.6
05:00		66	40	106	62.3
06:00		61	48	109	56.0
07:00		86	36	122	70.5
08:00		66	36	102	64.7
09:00-12:00	21.VI.1966	60	28	88	68.2
10:30	21.VI.1968	54	36	90	60.0
12:00	24.VI.1966	87	57	144	60.5
14:30	22.VI.1966	72	32	104	69.2
15:00	21.VI.1968	45	29	74	60.8
16:00	24.VI.1966	72	55	127	56.7
18:00	25.VI.1966	82	49	131	62.6
21:00	24.VI.1966	58	24	82	70.8
21:30	18.VI.1968	13	7	20	65.0
Total		1079	616	1695	63.66 Average



these flowers were Collembola, *Entomobrya comparata*.

VI.7.4.7.3. *Cerastium alpinum*

Hocking and Sharplin (1965) note that they measured the temperature within the corollas of this flower, Hocking (1968) recording a temperature excess of about 1 C.

On 28.VII.1966, 4 flowers were experimented on throughout a simulated 24 hours of sunlight. Fig. 41 and Appendix III-8-9 present the results. They are very similar to those obtained for *Saxifraga oppositifolia*. The flowers are white and slightly more open than the latter; this may account for the more delayed but steeper fall off.

These flowers are not well visited by insects. They may be frequented by small parasitic hymenoptera at times, and these may make use of the elevated temperatures as they remain in the flowers for long periods of time.

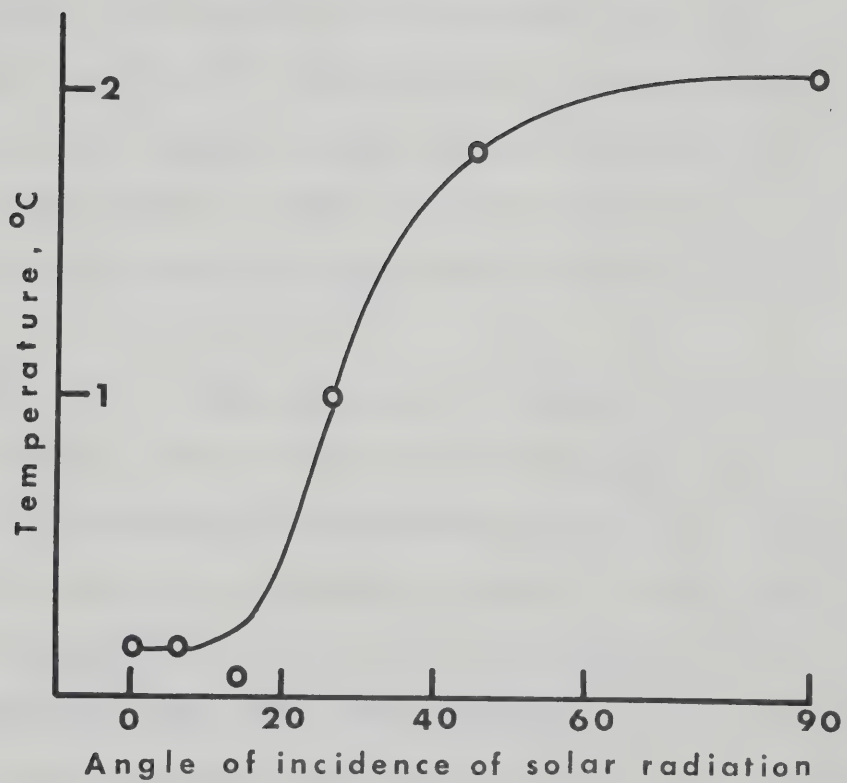




Figure 51.

Temperature excesses in flowers of *Cerastium alpinum* with respect to the angle of incidence of solar radiation. Experimental observations, Hazen Camp, 1966.







PART VII  
POLLINATION

VII.1. Introduction

Plants have evolved mechanisms for the attraction of animals to implement the distribution of either pollen grains or seeds. I have shown that most species of the Lake Hazen flora exhibit all, or nearly all, the attractive characteristics of insect pollinated plants of more temperate regions. Although this is not entirely new information, I have clarified a number of points which were in question and have been used in arguments against insect dependence on arctic flowers.

A great deal has been said about the tendency towards autogamy in arctic plants. Even shortly after the Darwin-Knight law of nature's abhorrence of perpetual self-fertilization, Aurivillius (1883) proposed autogamous reproduction in *Pedicularis lanata*. Ekstam's works (1897, 1899, 1894) expanded the ideas of increased autogamy in arctic flowers and Warming (1886, 1908, 1909, 1920), Mathiesen (1921), Jessen (1913), and others laid the foundations of what is upheld today. No authors have actually said that insect pollination does not occur, except as mentioned above. The quotation from Mosquin (1966) (see in II.1.1) summarizes present ideas in general. Ideas contrary to the above have been put forward by Chernov (1966), and evidence is given by Gavriluk (1961, 1966), Panfilov *et al.* (1960), and Shamurin (1962, 1966a, b) who cite examples of plants (particularly legumes) dependent on bumblebees and flies for pollination.





Figure 52.

Insect excluder in position over clumps of *Papaver radicatum*  
at Hazen Camp, 1968.







The plants experimented upon are listed below with the treatments used on each.

1) *Saxifraga oppositifolia*:

- 1966: 8 clumps, totalling 94 flowers collectively, without insect excluders, normal.
- 5 clumps, totalling 137 flowers collectively, with insect excluders, normal.
- 4 clumps, totalling 38 flowers collectively, without insect excluders, and emasculated.
- 1967: 7 clumps, totalling 98 flowers collectively, without insect excluders, normal.
- 10 clumps, totalling 109 flowers collectively, with insect excluders, normal.
- 4 clumps, totalling 28 flowers collectively, without insect excluders, and emasculated.
- 2 clumps, totalling 16 flowers collectively, with insect excluders, and emasculated.
- 1968: 7 clumps, totalling 124 flowers collectively, without insect excluders, normal.
- 6 clumps, totalling 60 flowers collectively, with insect excluders, normal.
- 3 clumps, totalling 19 flowers collectively, without insect excluders, and emasculated.
- 5 clumps, totalling 34 flowers collectively, with insect excluders, and emasculated.
- 2 clumps, totalling 22 flowers collectively, with insect excluders, normal, and pollinated by hand.
- 3 clumps, totalling 29 flowers collectively, with insect excluders, emasculated, and pollinated by hand.

2) *Saxifraga tricuspidata*:

- 1968: 2 clumps, totalling 84 flowers collectively, without insect insect excluders, normal.



2 clumps, totalling 35 flowers collectively, with insect excluders, normal.

3) *Dryas integrifolia*:

1967: 6 clumps, totalling 63 flowers collectively, without insect excluders, normal.

6 clumps, totalling 85 flowers collectively, with insect excluders, normal.

1968: 8 clumps, totalling 67 flowers collectively, without insect excluders, normal.

3 clumps, totalling 19 flowers collectively, with insect excluders, normal, and pollinated by hand.

1 clump, totalling 5 flowers, without insect excluder, and emasculated.

Other clumps were set up with combinations of treatments of insect excluders, emasculations and pollination by hand; these were eaten by arctic hares.

4) *Papaver radicatum*:

1966: 6 clumps, totalling 11 flowers collectively, without insect excluders, normal.

3 flowers, with insect excluders, normal.

1967: 2 flowers, without insect excluders, normal.

2 flowers, with insect excluders, normal.

1968: 2 clumps, totalling 10 flowers collectively, without insect excluders, normal.

5 clumps, totalling 30 flowers collectively, with insect excluders, normal.

5) *Taraxacum arctogenum*:

1968: 2 clumps, totalling 13 flowers collectively, without insect excluders, normal.

2 clumps, totalling 9 flowers collectively, with insect excluders, normal.



6) *Arnica alpina*:

1968: all devastated by arctic hares.

7) *Potentilla nivea*:

1968: all devastated by arctic hares.

8) *Epilobium latifolium*:

1968: 2 clumps, totalling 9 flowers collectively, without insect excluders, normal.

2 clumps, totalling 17 flowers collectively, with insect excluders, normal.

9) *Lesquerella arctica*:

1968: 3 clumps, totalling 93 flowers collectively, without insect excluders, normal.

4 clumps, totalling 135 flowers collectively, with insect excluders, normal.

10) *Erysimum Pallasii*:

1968: 1 plant with 9 flowers, without insect excluder, normal.

1 plant with 42 flowers, with insect excluder, normal.

11) *Cassiope tetragona*:

1968: 2 clumps, totalling 75 flowers collectively, without insect excluders, normal.

2 clumps, totalling 86 flowers collectively, with insect excluders, normal.

12) *Salix arctica*:

1966: 9 clumps, totalling 15 pistillate catkins collectively, without insect excluders.

9 clumps, totalling 12 pistillate catkins collectively, with insect excluders.





- 1967: 2 clumps, totalling 24 pistillate catkins collectively,  
without insect excluders.
- 2 clumps, totalling 26 pistillate catkins collectively,  
with insect excluders.
- 1968: 9 clumps, totalling 59 pistillate catkins collectively,  
without insect excluders.
- 5 clumps, totalling 42 pistillate catkins collectively,  
with insect excluders.
- 3 clumps, totalling 29 pistillate catkins collectively,  
with insect excluders, and pollinated by hand.

13) *Pedicularis arctica*:

- 1967: 3 clumps, totalling 7 plants, totalling 67 flowers  
collectively, without insect excluders, normal.
- 3 clumps, totalling 6 plants, totalling 67 flowers  
collectively, with insect excluders, normal.
- 1968: 1 plant, totalling 8 flowers, without insect excluder,  
normal.

Several clumps to duplicate the experiments of 1967 were  
all eaten overnight by arctic hares.

14) *Pedicularis capitata*:

- 1968: 6 plants, totalling 19 flowers, without insect excluders,  
normal.
- 5 plants, totalling 19 flowers, with insect excluders,  
normal.

The experimental plants were harvested at the end of the season,  
and returned to the laboratory for examination. The criteria used for  
seed production were as follows:

*Saxifraga* spp., *Pedicularis* spp., *P. radiculatum*, *C. tetragona*, and  
the Cruciferae with dehiscent seed pods or firm ripening pods indicated  
that seeds were produced; when pods were absent or withered and  
soft, indicating fertilization had not taken place, the remains of



the corollas were often evident (on some saxifrages shrivelled remains of stamens could also be seen).

*Salix arctica*, *Dryas integrifolia*, *Taraxacum arctogenum* and *Epilobium latifolium* with seed plumes indicated that seeds were produced. When plumes were not present in *S. arctica* and *E. latifolium* the pods were abortive and soft, in *Dryas integrifolia* seed plumes were sometimes much shorter, and the achene much smaller, than the long plumed achene taken as the normal fruit, the smaller fruits were regarded as abortive seeds\*, fruits were entirely absent from some flowers.

#### VII.2.3. Results

The results of the pollination experiments are given in Table 32.

#### VII.2.4. Conclusions

It is obvious which of the species tested are autogamous; they are *P. radicatum* (cf. Shamurin, 1962, *P. lapponicum* Tolm.), *T. arctogenum*, *L. arctica*, *E. Pallasii*, *E. latifolium*, all of which produced seed equally well whether or not insects were free to visit their flowers. Two plants with three flowers each of *Melandrium triflorum*, appeared to have had developing seed pods before they were eaten by hares, and similarly about 10 flowers of *Potentilla nivea* which Shamurin (1962) writes is pollinated by flies and not autogamous. Shamurin (l. cit.) also records *Melandrium apetalum*, *Saxifraga Hirculus*, and *S. flagellaris*

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\*Possibly these are halpoid seeds.



Table 32.

Results of pollination experiments as expressed by seed set around Hazen Camp.

Key:	<u>S -- with seeds</u>			<u>W -- without seeds</u>			<u>N -- number of plants</u>					
	<u>S</u>	<u>W</u>	<u>N</u>	<u>S</u>	<u>W</u>	<u>N</u>	<u>Normal flowers covered</u>		<u>Emasculated flowers not covered</u>		<u>Emasculated flowers covered</u>	
							<u>Normal flowers covered hand pollinated</u>		<u>Emasculated flowers covered hand pollinated</u>			
							<u>S</u>	<u>W</u>	<u>N</u>	<u>S</u>	<u>W</u>	<u>N</u>
<i>Saxifraga oppositifolia</i>												
1966	88	6	8	16	121	5			34	4	4	
1967	92	6	7	8	101	10			25	3	4	
1968	107	17	7	2	58	6			12	7	3	
Total	287	29	22	26	280	21			71	14	11	
<i>Saxifraga tricuspidata</i>												
1968	38	46	2	16	19	2						
<i>Epilobium latifolium</i>												
1968	6	3	2	15	2	2						
<i>Taraxacum arctogenum</i>												
1968	13	0	2	9	0	2						
<i>Dryas integrifolia</i>												
1967	48	15	6	28	57	6						



Table 32 (contd.).

		Key: S -- with seeds			W -- without seeds			N -- number of plants		
		Normal flowers not covered			Emasculated flowers not covered			Emasculated flowers covered		
		S	W	N	S	W	N	S	W	N
<i>Dryas integrifolia</i>										
1968	55	12	8	(31)	4	1	1	18	1	3
Total	103	27	14	28	4	1	1	18	1	3
<i>Papaver radicatum</i>										
1966	11	0	6	3						
1967	2	0	2	2						
1968	10	0	2	30						
Total	23	0	10	35						
<i>Lesquerella arctica</i>										
1968	93	0	3	135						
<i>Erysimum Pallasii</i>										
1968	9	0	1	42						
<i>Pedicularis arctica</i>										
1967	63	4	3	5						
1968	8	0	1							
Total	71	4	4	5						
<i>Pedicularis capitata</i>										
1968	15	4	6	0						





Table 32 (contd.).		Key: S -- with seeds			W -- without seeds			N -- number of plants					
	Normal flowers not covered	Normal flowers covered		Emasculated flowers not covered		Emasculated flowers covered		Normal flowers covered hand pollinated		Emasculated flowers covered hand pollinated			
		S	W	N	S	W	N	S	W	N	S	W	N
<i>Salix</i>													
<i>arctica</i>													
1966	14	1	9	0	12	9							
1967	24	0	2	0	26	2							
1968	41	18	9	0	42	5							
Total	79	19	20	0	80	16							

( ) Destroyed by hares



as autogamous and pollinated by flies, and *Cassiope tetragona* as autogamous (my incomplete results (not presented) from experiments on *C. tetragona* also indicate this to be true at Hazen Camp).

*S. tricuspidata* shows the same amount of seed set with or without the aid of insects, normally setting seed in less than 50% of its flowers. *S. oppositifolia*, on the other hand, has a seed set of less than 10% if insects are prohibited from visiting, while under natural conditions its seed set is well over 90%. This is not an artifact caused by the excluder as of the 51 flowers hand pollinated under the excluders 44 set seed, a seed set of 88%. The importance of insect pollination in this species is further emphasized by the 84% seed set in 85 emasculated flowers to which insects had access. Autogamous seed production in this species is less than 10%, but does occur; emasculated flowers within excluders failed to produce any seed.

*D. integrifolia* in the open has a seed set of 80%, but when insects are excluded from the flowers this drops to 33%. Again this is not an artifact of the excluders as hand pollinated flowers under them produced 95% seed set. Emasculation of these flowers is tedious work, so few were set up, and even fewer remained after arctic hares had feasted. Of the 5 which survived in the open 4 set seed, and of the 7 placed under excluders (which were subsequently knocked off by hares), 3 produced seeds. *D. integrifolia* appears dependent on insects to assure maximum seed set, but can develop seeds autogamously (cf. Shamurin, 1962 for *D. punctata* Juz.).

*Pedicularis capitata* appears to be entirely dependent on insects for seed set. The only pollinators of this species are bumblebees,



particularly workers of *Bombus polaris*. *P. arctica* is very much the same but can set 7% seed autogamously. The pollinators again are mainly bumblebees. Some arctic *Pedicularis* spp. are autogamous (MacInnes, pers. comm; Shamurin, 1962).

*Salix arctica* is entirely dependent on insects for seed production. It produces no seeds under the insect excluders, while having 78% success in the open. The lack of seed set under the cones is not an artifact as hand pollinated catkins developed very vigorously, growing in excess of 5 cm long, and having 100% seed set. This contradicts the idea expressed by Mosquin and Martin (1967) that the "arctic willow may well be losing a dependence on insect pollination and evolving towards wind pollination."

### VII.3. Pollinators at Hazen Camp

The ability to carry pollen grains is not enough to characterize a pollinating insect. Good pollinators must also visit more than one flower of the same species within the period of viability of the pollen grains they carry. They must also visit flowers in such a way as to pick up viable pollen and transfer it to the stigmas of subsequently visited flowers. Insects which are constant or steadfast to particular flowers, and behave as above, are more effective pollinators than insects which visit many kinds of flowers. McAlpine (1965) says that "probably 85 to 90% of the netted specimens taken from the Lake Hazen area have at least a few grains of pollen caught among the hairs on their bodies." Shamurin (1966a) discusses the roles of pollinators on the tundra and considers bumblebees the most effective pollinators, while Diptera are important too because of their high numbers. The primary importance





of bumblebees and secondary importance of Diptera as pollinators is brought out by Chernov (1966) and Gavriljuk (1966). Hocking (1968) considers that there is "competition between flowers for pollinators rather than among pollinators for nectar." Richards (1970: 114) upholds the claim that almost all entomophilous plants beyond the tree-line are self-fertile while suggesting a sympatric distribution of many bumblebee visited plants and bumblebees, mentioning in particular the absence of both *Dryas integrifolia* (perennial and self-fertile) and *Bombus* spp. from Ellef Ringnes Island (p. 115).

Table 33 presents my findings on the pollen carrying potential of the insects at Hazen Camp in terms of the per cent of the population of each species collected from flowers and carrying pollen.

From the species listed in Table 33, the most important pollinators are probably the Empididae, Syrphidae, Phaoniinae, *Spilogona* spp. and *Bombus* spp. and to lesser extents Tachinidae, *Boreellus atriceps*, *Aedes* spp., Lepidoptera, and *Smittia velutina*.

Table 34 shows the flowers dependent at least in part for maximum seed set, and the insects mostly responsible for their cross pollination.

Cross pollination, although unnecessary for reproduction or seed set must also occur to a variable extent in other flowers at Hazen Camp. Among these flowers are *Cerastium alpinum*, *Stellaria longipes*, *Papaver radicum*, *Draba Bellii*, *Erysimum Pallasii*, *Lesquerella arctica*, *Saxifraga Hirculus*, *Potentilla nivea*, *Epilobium latifolium*, *Arnica alpina*, *Taraxacum arctogenum*.



Table 33.

Per cent of each anthophilous species of arthropod found on flowers and dusted with pollen grains, Hazen Camp, 1967.

<u>Species</u>	<u>% carrying pollen</u>	<u>Number considered</u>
<i>Xysticus deichmanni</i>	50	22
other Araneida	25	12
<i>Apatania zonella</i>	0	1
<i>Anarta richardsoni</i>	63	8
<i>Crymodes exulis</i>	85	13
<i>Lasiestra leucocycla</i>	79	14
<i>Boloria polaris</i>	100	3
<i>B. chariclea</i>	88	8
Lycaenidae	20	5
other Lepidoptera	50	2
<i>Tipula arctica</i>	100	1
<i>Smittia</i> spp.	85	631
<i>Limnophyes</i> spp.	40	82
<i>Paraphaenocladus despectus</i>	40	20
other Chironomidae	44	25
<i>Aedes</i> sp.	77	22
<i>Bradysia</i> spp.	41	27
<i>Dolichopus dasyops</i>	0	3
<i>Rhamphomyia filicauda</i>	88	215
<i>R. nigrita</i>	85	44
<i>R. hoeli</i>	80	37
<i>Carposcalis carinata</i>	88	58
<i>Phalacrodira nigropilosa</i>	83	18
<i>Metasyrphus chillcotti</i>	88	8
<i>Helophilus borealis</i>	100	2
<i>Phytomyza erigontophaga</i>	20	5
<i>Boreellus atriceps</i>	35	47
<i>Peleteria aenea</i>	82	17
<i>Fucellia pictipennis</i>	40	5
<i>Eupogonomyia groenlandica</i>	55	11
<i>Pogonomyoides segnis</i>	93	28
<i>Pegomyia</i> spp.	100	2
<i>Spilogona melanosoma</i>	91	11
<i>S. sanctipauli</i>	95	40
<i>S. tundrae</i>	83	6
<i>Spilogona</i> other spp.	90	14
<i>Nematus</i> spp.	40	5
Parasitica	42	19
<i>Bombus</i> spp.	87	22
Average	69.2	Total 1706



Table 34.

Flowers dependent, at least in part, on insects for maximum seed set, and the insects mostly responsible for pollination at Hazen Camp.

Flower species

<i>Salix arctica</i>	<i>Carposcalis carinata</i> <i>Phalacrodira nigropilosa</i> <i>Bombus polaris</i> <i>Boreellus atriceps</i> * <i>Smittia velutina</i> **
<i>Saxifraga oppositifolia</i>	<i>Carposcalis carinata</i> <i>Phalacrodira nigropilosa</i> <i>Bombus polaris</i> (Q) <i>Boreellus atriceps</i> * <i>Smittia velutina</i> **
<i>Dryas integrifolia</i>	<i>Rhamphomyia nigrata</i> <i>R. filicauda</i> <i>Eupogonomyia groenlandica</i> <i>Pogonomyoides segnis</i> <i>Spilogona sanctipauli</i> <i>S. melanosma</i> <i>Spilogona</i> spp. <i>Bombus polaris</i> (W) Lepidoptera <i>Aedes</i> spp. <i>Carposcalis carinata</i>
<i>Pedicularis arctica</i>	<i>Bombus</i> spp. (mainly <i>polaris</i> )
<i>P. capitata</i>	<i>Bombus</i> spp. (mainly <i>polaris</i> )

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\* McAlpine (1965) states that *Boreellus atriceps* is usually well dusted with pollen, while I recorded only 35% carrying pollen. This discrepancy is not understood (see part IV-21).

\*\* Individuals of *Smittia velutina* may or may not visit more than one inflorescence in their lifetimes. If the latter is true they cannot be pollinators.





From the foregoing discussion and from Part IV "Arthropods on Flowers", it is obvious that bumblebees are not the all important pollen vectors. The Diptera are particularly important as they exhibit obligatory flower constancy or steadfastness due to the preponderance of flowers of one species available at one time. To Diptera, the season starts with *Saxifraga oppositifolia*, changes to *Salix arctica*, then to *Dryas integrifolia*, and at Gilman Camp this is followed by *Arnica alpina*. At Hazen Camp, after the finish of the *Dryas integrifolia* bloom, no single species of flower is dominant, *Stellaria longipes*, *Cerastium alpinum*, *Polygonum viviparum*, *Saxifraga Hirculus*, and others are all in bloom with late flowering plants of previously mentioned species.

The Diptera regarded as important pollinators all visit more than one inflorescence of each plant, as many observations have shown. Certainly McAlpine's (1965b) mention of the high proportion of netted specimens carrying pollen is circumstantial evidence for this argument. When visiting pleomorphic flowers, Diptera feed on nectar in any of three positions, none of which are constant to any species. The important pair of positions in ducking for nectar are firstly so that the notum rubs the anthers and secondly so that the notum touches the stigmas. In this way they cannot help but transfer pollen. On secondarily actinomorphic flowers, insect visitors become well dusted beneath and must transfer pollen from anthers to stigmas within and without the same inflorescence. On rhopalomorphic inflorescences of *Salix arctica* visiting insects cannot help but become dusted with pollen from staminate catkins and transfer pollen to the stigmas of pistillate catkins.

Only the large zygomorphic flowers (*Pedicularis* spp.) are dependent





on *Bombus* spp. at Hazen Camp. In other parts of the arctic, *Helophilus* spp. may be important pollinators of *Pedicularis* spp. (MacInnes, pers. comm.). Mosquin and Martin (1907) and Savile (in Mosquin and Martin, 1967) suggest *Pedicularis* spp. are strongly self-pollinated, but this clearly requires investigation.

#### VII.4. Regional Differences in Seed-set and Pollination in the Hazen Camp Area

##### VII.4.1. Aim

The aim of the following observation was to determine whether different regions of the Hazen Camp study area differed in the proportion of flowers setting seed in them.

##### VII.4.2. Methods and Materials

On 4.VIII.1968, I walked about 25 km over the Hazen Camp study area (Fig. 3) and in each quadrant crossed, I counted the seed heads of *Dryas integrifolia*, noting the number of well developed heads and the number of reduced or abortive heads in one square meter. To avoid bias in sampling when I arrived in the region to be surveyed I closed my eyes, disorientated myself by turning round several times, threw three meter sticks in the air, and took counts between the 2 meter sticks lying closer together. I used the meter sticks to delimit the square meter. At the same place, I noted the proximity of water and aridity.

I also counted heads of *Salix arctica* in a few areas.

##### VII.4.3. Results

The results are presented in Table 35.



Table 35.

Per cent seed set in *Dryas integrifolia* in different regions of the Hazen Camp study area in 1968.

Region and quadrat number (Fig. 3)	% with well developed seed heads	Number of samples	Number of flowers
A. Along water courses with sedgy areas (E8,F8,G8,M8, J8, P9, S7, S6)	84	8	322
B. Near ponds (P10, N11, L10, D9, M2, L3, T6, R5)	78	8	304
C. Near ponds (N12, Q5)	54	2	111
D. Near intermittent streams, short distance from water (R8,S7, N3, M4, L8, M9, M10, N10, K10, L12, K13)	62	11	531
E. In Blister Creek delta (J14, H15, G15, F14, E13, D12)	51	6	232
F. In dry areas (N2, P4, L6, L7, J9, D10, D11)	36	7	279
In dry areas (M5)	53	1	43
Total		43	1822

#### VII.4.4. Discussion and Conclusions

A t test was applied to the results to determine the significance of the differences seen in each region (see Table 36).



Table 36.

Results of t tests applied to per cent seed set in *Dryas integrifolia* in different regions of the Hazen Camp study area (see Table 35).

Regions A to F as in Table 35.

S, significantly different ( $P < 0.05$ ).

S\*, significantly different ( $P < 0.1$ ).

I, insignificantly different ( $P > 0.1$ ).

	B	C	D	E	F
A	I	S	S	S	S
B		S	S	S	S
C			I	I	-
D				I	S
E					S*

It is clear that in regions along water courses with sedgy areas and near ponds, *Dryas integrifolia* produces significantly more seed than in other regions. There are exceptions in some regions near ponds, but the reasons for this are not understood. It is interesting that in Blister Creek delta, for all its abundant water, *D. integrifolia* has significantly lower seed-set. I think that this reflects the unsuitability of the gravel and sand washed down by the glacial melt water for most insects, particularly pollinators of *D. integrifolia*. Pollination experiments alone in this region showed uncovered inflorescences of *Salix arctica* and *Saxifraga oppositifolia* produce large numbers of seeds. This may reflect the lack of availability of other nectar producing plants elsewhere when *S. arctica* and *S. oppositifolia* are in bloom.

Near intermittent streams and short distances from water, *D. integrifolia* showed good seed-set, but significantly fewer seeds were produced than near sedgy areas. In dry regions, where *Kobresia*





*myosuroides* (Vill.) is abundant, the seed-set of *D. integrifolia* was significantly the lowest.

*Salix arctica* was examined only in wet areas (F9, E9, G9, H14) where 83% of the catkins produced seeds. Similar success was apparent from uncovered catkins used as controls in the pollination experiments in Q9, P10, P11, N4, and H15.

I could detect no difference in the abortive seed heads of *Dryas integrifolia* which had resulted from plants being under insect excluders from those which developed (or failed to develop) in regions of low seed-set. Therefore I interpret my results to reflect the suitability of different regions for pollinators, and hence the availability and abundance of them. Thus flowers of *D. integrifolia* do compete for pollinators (*cf.* Hocking, 1968), particularly outside regions of abundant pollinators. Competition for pollinators may also be reflected in the few inflorescences of various flowers dependent on insects not setting seed although uncovered.



PART VIII

DISCUSSION AND CONCLUSIONS

Before discussing floral attractants it is necessary to erect a table of insect abundance on each species of flower. The number of visits of insect to each flower has not been considered, as it does not take into account differences in abundance of different species of insects equally dependent on flowers. The number of species has not been used because of taxonomic difficulties at the species level in some groups. I have used the number of genera because most insects were identifiable to this level, and many genera are monotypic at Hazen Camp; also, the species of polytypic genera are closely related with respect to their relationships with flowers (e.g. *Smittia* spp., *Limmophyes* spp., *Aedes* spp., *Bradysia* spp., *Rhamphomyia* spp., *Spilogona* spp., *Bombus* spp.) that it is natural to regard such genera as units. I have also presented the abundance of different families on each species of flower, but this is not as meaningful as the generic abundance. For instance, the biologies of the genera of Chironomidae, Syrphidae, Muscidae, and Noctuidae are different with respect to their relationships with flowers. Table 38 shows the generic and familial abundance of insects on each species of flower.

*Dryas integrifolia* is the most diversely visited flower, followed by the inflorescences of *Saxifraga oppositifolia*, *Salix arctica*, *Arnica alpina*, and *Potentilla nivea*, all of which were visited by more than 14 genera and 10 families of arthropods. These are the most entomophilous inflorescences. There are 7 other species of plant with entomophilous inflorescences which were visited by between 8



and 13 genera. Then follow 19 species of plant (including *Draba* spp. and *Braya* spp. as 1 species each) which show markedly less entomophily, having been visited by 1 to 4 genera or families of insects. This group can be subdivided into 3 (see Table 38). Finally there are a few showy inflorescences from which, because of their comparative scarcity, I recorded no visitors (some *Taraxacum* spp., some *Potentilla* spp.); and a number of plants with inconspicuous inflorescences (Monocotyledons, *Oxyria digyna*, *Armeria maritima*, some *Ranunculus* spp., *Hippurus vulgaris*, some *Saxifraga* spp., *Arenaria* spp., some *Cruciferae*, and *Epilobium davuricum*). Table 37 gives the criteria for the degree of entomophily used in Table 38.

Table 37.

Numbers of different genera and different families of arthropods from different inflorescences and the corresponding degree of entomophily as used in Table 38. (Data from Hazen Camp, 1966, 1967, 1968).

Visitors Recorded			
<u>Degree of entomophily</u>	<u>Number of families of arthropods</u>	<u>Number of genera of arthropods</u>	<u>Comments</u>
1 most	10 or more	15 or more	
2 fair	7 - 11	8 - 13	
3	2 - 4	2 - 4	visitors few, and infrequent
4	1 - 3	1 - 3	at least one consistent visitor
5	1 - 2	1 - 2	visitors rare
6	0	0	no visitors recorded



Table 38.

Entomophily in the Lake Hazen flora. Numbers of different families and genera associated with different species of flowers.

		Arthropod Visitors			
Degree of ento- mophily	Species of inflorescence	No. of fam.	No. of Gen.	(Hocking, 1969) No. of fam. No. of gen.	
1	<i>Dryas integrifolia</i>	21	42	16	28
	<i>Saxifraga oppositifolia</i>	16	25	9	21
	<i>Arnica alpina</i>	17	23	4	4
	<i>Salix arctica</i> (staminate)	14	20	13	17
	<i>Salix arctica</i> (pistillate)	10	17	8	10
	<i>Potentilla nivea</i>	12	15	10	10
2	<i>Stellaria longipes</i>	6	6	8	10
	<i>Pedicularis arctica</i>	7	11	1	1
	<i>Polygonum viviparum</i>	7	11	1	1
	<i>Papaver radicatum</i>	8	11	5	7
	<i>Taraxacum arctogenum</i>	8(9)	8(9)	4	4
	<i>Lesquerella arctica</i>	8	9	4	4
3	<i>Cerastium alpinum</i>	1(4)	1(4)	2	3
	<i>Draba Bellii</i>	0(3)	0(3)	1	1
	<i>Saxifraga tricuspidata</i>	0(3)	0(3)	4	4
	<i>S. Hirculus</i>	3	3	2	2
	<i>Erysimum Pallasii</i>	2(3)	2(3)	3	3
	<i>Chrysanthemum integrifolium</i>	0(2)	0(3)	0	0
	<i>Epilobium latifolium</i>	0(2)	0(2)	4	4
4	<i>Pedicularis capitata</i>	1(2)	1(2)	1	1
	<i>P. hirsuta</i>	--	--		
	<i>Erigeron compositus</i>	1	1		
5	<i>Draba</i> spp. (all but <i>Bellii</i> )	2	2	1	1
	<i>Braya</i> spp.	9(1)	0(1)	1	2
	<i>Cassiope tetragona</i>	0(1)	0(1)	3	3
	<i>Melandrium triflorum</i>	0(1)	0(1)	1	2
	<i>Saxifraga cernua</i>	0	0	1	1
	<i>Saxifraga fragellaris</i>	0	0	1	1
	<i>Silene acaulis</i>	0	0	1	1
	<i>Erigeron eriocephalus</i>	1	1	0	0
	<i>Cerastium arcticum</i>	0	0	1	1
	<i>Ranunculus sulphureus</i>	1	1	0	0

Numbers in brackets are amendments to the 1967 data and are based on observation gathered in 1966 and 1968.





Hocking's (1968) results from 1963 are included in Table 38. In general both sets of results are in close agreement. Notable exceptions are *Arnica alpina*, found only occasionally above 400 m on the slopes of Mt. McGill, some 3.5 km from Hazen Camp, but growing abundantly at Gilman Camp where I spent 2 days in 1966 and 10 days in 1967 studying its visitors; *Pedicularis arctica* from which Hocking recorded 1 genus, *Bombus*, against the 11 I collected, most from within the flowers and hence invisible externally; and *Polygonum viviparum* which may not have bloomed profusely in 1963 (in 1967 most of the insects from these inflorescences were collected within a 3 day period at the end of the season); other differences are unimportant, and probably reflect any of faunal and floral differences, differences in collection techniques, and differences in our respective lucks.

All genera and families of arthropods collected on the different inflorescences are counted in Table 38. Some records are spurious, these are some of the Acarina, Araneida, and Chironomidae, but deletion of these does not alter the degree of entomophily of any inflorescence. *Dryas integrifolia* is most affected, by about 7 genera, followed by the other inflorescences with high degrees of entomophily. However I could not always determine whether particular insects were spurious visitors, or specimens of uncommon anthophilous species.

Some amendments to Table 38 were necessary due to observations from 1968 and 1966. *Pedicularis capitata* did not bloom profusely in 1967. In 1968 I added visitors to *Epilobium latifolium*, *Cerastium alpinum*, *Cassiope tetragona*, *Melandrium triflorum*, while 1966 and 1968 I found insects on *Saxifraga tricuspidata*. Hocking (1968) also listed one visiting insect to each of *Saxifraga flagellaris*, *S. cernua*, and



*Cerastium arcticum*.

The colours of the inflorescences exhibiting high degrees of entomophily range from insect-dull-blue-black on insect-grey (pistillate catkins of *Salix arctica*) to bright insect-yellow (*Stellaria longipes*) and from insect-dull-blue (*Saxifraga oppositifolia*) to insect-pinks and -reds (creamy and yellow flowers without ultraviolet) and insect-two-tone-red-and-mauve (*Arnica alpina* and *Taraxacum arctogenum*).

Of the 32 species of white (or insect-yellow) flowers at Hazen Camp, only 2, *S. longipes* and *Polygonum viviparum* show relatively high entomophily, and 1 other, *Cerastium alpinum* shows some entomophily; all others, some of which (e.g. *Melandrium triflorum*, *Cassiope tetragona*, *Saxifraga cernua*) are as conspicuous as other highly entomophilous inflorescences, show very little or no entomophily. The reason for this is complex, and not fully understood. White (insect-yellow) seems unattractive to insects. *S. longipes* owes its entomophily mainly to 8 genera of Parasitica, otherwise it is infrequently visited by few insects, similar is *C. alpinum*. Most of the insects collected from *S. longipes* came from flowers growing in marshes of ponds and stream beds. *Polygonum viviparum* owes its entomophily to its late blooming; it is rarely visited while other inflorescences are available. Certainly such inflorescences as *Draba groenlandica*, *Braya humilis*, and flowers of *Melandrium triflorum* are as conspicuous as those of *P. viviparum* and *D. Bellii* (yellow), but none of them are visited by insects while other flowers abound. All white flowers are of approximately equal colour saturation (75 to 100%), about the same as most other entomophilous flowers of other colours.

Among the purple flowers, there are differences in ultraviolet





(insect-blue) reflection. Flowers of *S. oppositifolia* and *Erysimum Pallasii* are almost identical, reflecting none, while those of *Epilobium latifolium* reflect about 20%. All three reflect similarly in the insect-blue and insect-green part of the spectrum, *S. oppositifolia* and *E. Pallasii* at 45% in each, while *E. latifolium* is stronger in the insect-blue (55%) but weaker in insect-green (35%). Insect-yellow and insect-orange are almost completely absorbed by all three, while in insect-red (yellow-orange) the flowers are slightly more reflective; reflection increases into the red (invisible to insects) part of the spectrum. Thus all three flowers are more or less insect-blue to insect-blue-green, possibly with tinges of insect-purple. All are relatively unsaturated in a region of the insect visual spectrum in which insects have lower sensitivities (*cf.* Weiss, 1944; Daumer, 1956; Goldsmith, 1961). Hence I would expect these flowers to be unattractive to insects for the same reason Mosquin and Martin (1967) propose *Astragalus alpinus* is not attractive to flies, i.e. their flowers have about the same reflectivity as adjacent greenery. The high degree of entomophily of *S. oppositifolia* is due to its being the only widespread flower in bloom at the start of the season. The number of visitors to *S. oppositifolia* diminishes markedly as soon as *Salix arctica* blooms, and the same species of insects are then found on its catkins. The chironomids are the only group to persist on *S. oppositifolia*, but they too abound on catkins. I cannot explain why female catkins (insect-grey with insect-dull blue-black stigmas) are so attractive in terms of colour or saturation. *Pedicularis arctica* and *P. hirsuta* are similar to *S. oppositifolia* and *E. Pallasii*, but reflect slightly more in the insect yellow-orange, and are highly saturated in the





insect red. Much of the apparent entomophily of *P. arctica* comes from 7 genera of Nematocera which were only occasionally recorded.

There are 23 species of yellow (insect-red) reflecting inflorescences, and of these 7 are highly entomophilous, 4 others show some entomophily (degree 3), 2 have one consistent visitor, 7 were not considered as they were not common enough to be examined frequently, and 3 are almost non-entomophilous. Thus almost all inflorescences reflecting insect-red are visited by insects, whether or not they also reflect other colours. Flowers of *Dryas integrifolia* have insect-orange petals with insect-red sporophylls, while flowers of *Papaver radicum* are insect red to insect-red-orange, pure insect-red flowers are *Lesquerella arctica*, *Draba Bellii*, *Potentilla* spp., *Saxifraga flagellaris*, and the disc florets or central florets of the Compositae. Ultraviolet is reflected by few flowers, notably by the distal parts of the petals of *Saxifraga Hirculus*, *Ranunculus sulphureus*, and the ray or peripheral florets of *Arnica alpina* and *Taraxacum arctogenum*, and weakly by parts of the galea of *Pedicularis capitata*, these ultraviolet (or insect-blue) reflecting parts are insect-purple (insect-purple = insect-red + insect-blue). Ultraviolet seems very attractive to insects (cf. Weiss, 1943, 1944; Daumer, 1956; Goldsmith, 1961, and Part V ) but as a floral attractant for insects in the high arctic it seems unimportant. *R. sulphureus* is hardly ever visited, and *S. Hirculus* owes its popularity to 2 genera of Parasitica also found on *Stellaria longipes*. Insect-violet patterns must make the flowers of different species distinguishable, but the importance of this around Hazen Camp is unknown.

It is interesting that Compositae with white ray florets (insect-



yellow) and yellow (insect-red) discs are not well visited. *Chrysanthemum integrifolium* owes its entomophily to 3 genera of insect collected from its inflorescences late in 1968 at Tanquary Fiord when most of the other flowers had finished blooming. *Erigeron compositus* is consistently visited by *Phytomyza erigerontophaga*, whose larvae mine the leaves of this plant, but other visitors are rare. I found only one chironomid on *E. eriocephalus*.

The sizes of inflorescences (as measured by their total outline lengths or circumferences; including extra length due to double colourations) have definite effects on their relative entomophilies. The smallest flowers falling into classes 1 and 2, i.e. less than 3.0 cm in circumference are not well visited. Into these classes fall *Polygonum viviparum*, *Arenaria rubella*, most *Ranunculus* spp., most Cruciferae, some *Saxifraga* spp., and *Cassiope tetragona*. Of these *P. viviparum* flowers form a tight rhopalomorphic spike of great, but indeterminate outline length, and *Draba Bellii* forms tight flowering heads which function as attractive units. The remainder are either not at all entomophilous (*A. rubella*, *Ranunculus* spp., *Saxifraga* spp.) or weakly so (some *Draba* spp., *Braya* spp., *C. tetragona*). Flowers with medium total circumferences (class 3) are *Stellaria longipes*, 2 *Braya* spp., and 4 *Saxifraga* spp. of which only the first mentioned is entomophilous, and then fortuitously so (see above). All the highly entomophilous inflorescences fall into classes 4 and 5 with relatively large total circumference (over 5 cm), but not all inflorescences this large are highly entomophilous; for example, *Erigeron* spp., *Chrysanthemum integrifolium*, *Epilobium latifolium*, some *Saxifraga* spp., most Caryophyllaceae, and *Pedicularis capitata* are rarely visited



by insects.

Although large size seems important for attracting insects, it is not enough in itself, and is subservient to colour. The explanation for this may lie in Manning's (1956b) remarks on the greater attractiveness to insects of longer lines of colour contrast on flowers.

Just as large total circumferences, must be more noticeable to insects because of the greater optical stimulation, inflorescences in motion due to wind must be more noticeable, and hence possibly more attractive. Extra stimulation to the insects' eyes would also come about through flicker. Immobile or stiff inflorescences are not attractive, with the exceptions of *Lesquerella arctica*, *Draba Bellii*, *Stellaria longipes*, and *Pedicularis arctica*. The most entomophilous flowers all move, but not all flowers which move are entomophilous. Movement is the product of inflorescence and stem sizes, and may be entirely incidental.

Flower form and figure numeral are not as important as other attractants. Of the secondarily amorphic inflorescences, not all are entomophilous, *Silene acaulis* because of its colour, and *S. oppositifolia* only if no other inflorescences are available. *Draba Bellii*, with its very small flowers, owes its entomophily to its colour and growth form (*cf.* Tikhomirov, 1959). Pleomorphy itself is not attractive. Strongly stereomorphic flowers are rarely, if ever, visited (flowers with medium and weak stereomorphy are included in the pleomorphic class). The secondarily actinomorphic inflorescences are not all entomophilous (e.g. *Erigeron eriocephalus*, *E. compositus*). Form numeral seems to have little importance in the attractiveness of flowers. Most of those with the form numeral 4 are Cruciferae, of which *Lesquerella arctica* is relatively highly entomophilous, and *Erysimum Pallasii* and *Draba Bellii*





are less so, the remaining Cruciferae being slightly or not entomophilous. *Papaver radicatum* also has a form numeral of 4 and is fairly entomophilous.

*D. integrifolia* and *Epilobium latifolium* have form numerals of 8; in the latter the pattern is easily resolvable into 2 patterns of 4 each. The form numeral 5 is common due to the Rosales, some of which are highly entomophilous (*Saxifraga oppositifolia*, *Potentilla nivea*), while others are not at all entomophilous (some *Saxifragaceae*). The *Ranunculaceae*, *Arenaria rubella*, and *Melandrium* spp. are not entomophilous and have also form numerals of 5. Other Caryophyllaceae (e.g. *Stellaria longipes*, and *Cerastium* spp.) have form numerals of 10 due to the divisions of the petals; they have a wide range of degree of entomophily.

The florets of the Compositae are zygomorphic but to insects can hardly be recognized as such. The flowers appearing zygomorphic to insects are *Pedicularis* spp., none of which are non-entomophilous. *P. arctica* is widely visited (but see above), and *P. capitata* and *P. hirsuta* are visited by bumblebees.

The rhopalomorphic inflorescences are entomophilous as is demonstrated by the numbers of visitors to both staminate and pistillate catkins of *Salix arctica*, *Polygonum viviparum*, and *Pedicularis arctica*; *Erysimum Pallasii* also shows some entomophily.

Honey guides are probably of little importance as attractants, and it is likely that the species with red markings (insect-black) are unattractive. Some visual honey guides may be important in aiding small insects to find nectar, and the structural honey guides of *Pedicularis* spp. probably aid bumblebees, their pollinators, in obtaining food.





Visual attractants of inflorescences to insects can be ranked according to their importance. Colour is of primary importance, yellow (insect-red) being the most attractive whether or not in combination with ultraviolet (insect-violet); in combination with white (e.g. *C. integrifolium* and *Erigeron* spp.) the apparent unattractiveness of white seems to over-ride, but scent may also be important (see below). White (insect-yellow) inflorescences, like purple (insect-blues) are unattractive unless there are no other inflorescences available. The reason for the unattractiveness of purple flowers is that they are relatively unsaturated in a part of the spectrum not particularly stimulatory to insect eyes. I do not understand the lack of insect visitors to some of the fairly abundant conspicuous white flowers, the saturations of the insect-red inflorescences and the insect-yellow ones is about equal.

Size too is important, small flowers not being attractive unless they grow in mats (secondarily amorphic) in spikes, etc (rhopalomorphic), while larger individually growing flowers tend to be attractive. Size seems subservient to colour, thus large white or purple flowers remain unattractive. Movement of inflorescences may play a small role in attracting insects, but around Hazen Camp it is probably not important.

The forms of inflorescences and figure numerals do not seem to play an important role in attracting insects, but may help anthophilous insects to recognize food providing inflorescences. Honey guides are also unimportant, except in possibly guiding some small insects to food, and to insects, particularly *Bombus* spp., visiting *Pedicularis* spp.

Although several authors have reported that arctic inflorescences



are odourless or have reduced odour, I found that most of those which I examined produce it. Some are strongly scented, particularly on warm sunny days of great insect activity. Nevertheless, odour does not seem to be an important attractant to insects, especially over long distances, but may be important at close range (less than 5 cm) to entice settling (Butler, 1951). Floral odours may help some insects (e.g. *Bombus* spp., Syrphidae) to determine whether flowers are physiologically ripe for providing food. Most of the odours of high arctic flowers are sweet. However, the conspicuous white inflorescences (white in combination with yellow included) have distinctive odours, the Compositae smelling of daisy, the *Melandrium* spp. of typical bitter-sweet campion scent, *Cassiope tetragona* smells heathy, and in most of the Cruciferae I could detect only the general plant odour. Perhaps this accounts for the lack of attractiveness of white flowers. *Taraxacum arctogenum* and *Papaver radiculatum* also have distinctive odours, and Hocking (1968) recorded *Silene acaulis* as "sweet aromatic." There is a trend for the highly entomophilous inflorescences to be more scented. Those showing the highest degree of entomophily all have odours of strength 2 or more. Strong scent may account for the otherwise apparently unentomophilous pistillate inflorescences of *Salix arctica* being so well visited.

Convection currents from flowers are considered briefly as attractive, in their own right or in carrying off odour.

Pollen is highly nutritive food for insects, but is not widely used. It is produced in great quantities, the most entomophilous inflorescences producing the most pollen. There are exceptions to this generality: *Epilobium latifolium* produces lots of pollen (the





grains are attached by threads of viscin) but is not highly entomophilous; and *Taraxacum arctogenum* and *Polygonum viviparum* are relatively more entomophilous but produce little pollen. There are several non-entomophilous plants which produce very little pollen.

There are 7 species of insect which feed on pollen direct from the anthers, and 2 (*Bombus* spp.) which remove pollen to feed their larvae. All the individuals of *Entomobrya comparata*, over 90% of the syrphid population (3 species examined; the other probably also feeds on pollen) and 70% of the females of *Pogonomyoides segnis* had pollen in their guts (males of *P. segnis* do not feed on pollen). All the above, except possibly the bumblebees and collembolans feed on pollen throughout their adult lives. Pollen feeding by the larvae of *Bombus* spp. is vital, and judging from the large proportions of the other pollen eating species with pollen in their guts, I propose that it is just as vital to them as food for maturation of gonads and general body maintenance.

The importance of nectar to insects, particularly as fuel for flight is well documented in Hocking (1953) and Elton (1966). Hocking's (1953, 1968) work on nectar secretion in the sub-arctic and taiga, and arctic respectively provides valuable insight into the importance of nectar secretion. From these data it can be calculated\* that the energy available from nectar at Churchill is about  $5.5 \times 10^3$  cal/m<sup>2</sup>/season and at Hazen Camp about  $3.7 \times 10^3$  cal/m<sup>2</sup>/season. Hocking's method of measuring nectar secretion is not absolutely accurate as he enclosed most of the plants under small plastic cones which act as

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\* Assuming an energy equivalent of  $3.59 \times 10^3$  cal/gm for glucose.





greenhouses. Some nectar concentrations which I measured are different under natural conditions.

Hocking recorded between 28 and 34% of the about 250 species of arthropods at Hazen Camp associated with flowers in 1963. I recorded about 44% of the species of arthropods associated with flowers. Of these, 4% (Arachnida) do not feed on nectar, and about 4% more are probably spurious visitors. Thus, at least 36% of the Hazen insect fauna feeds on nectar from flowers. Full examination over more years would probably show that all the Lepidoptera, Brachycera, and Hymenoptera, all the species of some families of Nematocera (Ceratopogonidae, Culicidae, Sciaridae) and some species of Chironomidae (*Limmophyes* spp., *Smittia* spp., *Corynoneura* sp. *scutellata*, and *Paraphaenocladus despectus*) and perhaps the collembolan (*Entomobrya comparata*) feed on nectar, on which they depend for fuel for locomotion and body maintenance. In many insect species aspects of their biologies and adaptations to the arctic can be interpreted from their nectar feeding habits.

Ovarian tissue of plants is used as food by a variety of arthropods (Acarina, and larvae of Lepidoptera, Diptera, and possibly Hymenoptera) but few are restricted to it for dietary requirements. Possibly dependent on ovarian tissue for sustenance are *Sympistris labradoris*, Tenthredinidae, Cecidomyiidae, and perhaps some seed eating Microhymenoptera.

Inflorescences may also serve as places for copulation (*Phytomyza erigerontophaga*) or as swarm markers for some Chironomidae. They also serve as ambush sites for some predators, among which *Xysticus deichmanni* is most abundant, followed by *Scatophaga apicaulis*. Males of *Rhamphomyia filicauda* capture their prey for courting gifts in flowers. To these 3 predators, flowers are probably indispensable as ambush sites. Other



predators found in flowers include spiders and the ascid mites. Death may also come to anthophilous insects associated with inflorescences through mermythid parasites or fungus diseases (*Etmophthora muscae*), but this likely has no relation to the plants.

Flowers, particularly if heliotropic, may serve as vantage points for visiting insects. They are forewarned of approaching potential danger in that its shadow arrives over the flower before the threat itself.

Elevated temperatures develop within inflorescences under direct solar radiation. The way in which these temperature excesses develop divides the flora into 6 categories: microgreenhouses, hairy heat traps, bells, discs, parabolic reflectors, and inverted bells. Microgreenhouses (*Pedicularis* spp. and *Melandrium* spp.) and hairy heat traps (*Salix arctica*) function similarly, absorbing short wave radiation and re-radiating it as long wave radiation which becomes trapped within the inflorescences (cf. Krog, 1955). Temperature excesses in microgreenhouse inflorescences depend on solar aspect, and under optimal conditions often exceed 5 C. Bells too must function partially as microgreenhouses, but probably depend more on convected warmth from the ground (cf. Büdel, 1959a, b). Only 1 small flower, *Cassiope tetragona* (around Hazen Camp) fits this category and temperature excesses rarely exceed 2 C. Discs (Compositae) are warmed directly by the sun, and their temperature excesses, sometimes over 6 C, under optimal conditions, fall off with the sine of solar incidence. Parabolic reflectors concentrate heat at their principal foci, the stigmas, and so become warmed. Temperature excesses usually lie between 5 and 10 C under optimal conditions and fall off with decreasing angles of solar



incidence, but not exactly according to the sine. Some parabolic flowers, notably *Dryas integrifolia* and *Papaver radicatum* are heliotropic, for part of the day and the whole day respectively. Therefore they must hold maximum temperature excesses for as long as they face directly into the sun. Stationary flowers such as *Ranunculus sulphureus*, *Potentilla* spp. are warmer for shorter periods. Winds over 3 or 4 mps remove all temperature excess from flowers of *D. integrifolia*. Inverted bells (e.g. *Saxifraga oppositifolia*, *Cerastium alpinum*, *Lesquerella arctica*) function similarly to parabolic reflectors, except that their deeper corollas and different shapes alter the effect of the angle of solar incidence. Temperature excesses rarely exceed 5 C. All flowers lose their temperature excesses in cloudy weather or under shade.

A variety of different arthropods visit inflorescences with temperature excesses, and benefit therefrom. The hairy heat traps are used mostly by Chironomidae, which must attain body temperature excesses at least as high as that of the inflorescence. *Pedicularis* spp. are probably not important in warming insects as relatively few are found within the corollas. *Cassiope tetragona* is rarely visited. The temperature excesses of disc inflorescences may be used by basking arthropods: *Phytomyza erigerontophaga* remains on the heads of *Erigeron compositus* for extended periods, and *Xysticus deichmanni*, numerous insects including Diptera and Lipidoptera (*vide* Kevan and Shorthouse, in press) apparently bask on *Arnica alpina*. Parabolic reflectors, particularly *D. integrifolia*, are well used by basking insects, especially by the Empididae, Culicidae, Syrphidae, and Muscidae. These attain body temperature excesses from 5.0 C and 16.7 C (depending on their





sizes) when resting in entire flowers of *D. integrifolia*. In the inverted bells of *S. oppositifolia* some Chironomidae (*Smittia* spp., *Limmophyes* spp., and *Paraphaenocladus despectus*) have constantly shifting populations, moving around clumps of flowers to remain on the insulated side.

In both the inverted bells and parabolic reflectors I showed that the petals are primarily responsible for temperature excesses. Flowers with the petals removed are much cooler than whole flowers, and the body temperature excesses of insects placed in decorollate flowers suffer accordingly.

Thus I have shown the importance to insects of the temperature excesses in flowers and proved that a "warm shelter" is "tenable" and of great significance to some insects in the arctic (see Part VI; and Faegri and van der Pijl, 1963: 58, 71).

Not only are floral temperature excesses important to insects, they must also be valuable to plants. Extra heat, important in a geographic region of low heat budget, must hasten growth and maturation of the sporophylls, hasten pollen tube growth, fertilization, and ovule development. Nectar secretion would tend to be increased (*cf.* Beutler, 1953; Blüdel, 1956, 1957, 1959a, b; Hocking, 1953; Shuel, 1967) and so increase the visits of insects. Possibly the convection currents generated could attract insects directly or indirectly by carrying off more odour further, enticing them to settle.

There is a distinct relation between the development of temperature excesses and entomophily. All the most highly entomophilous inflorescences develop fairly high temperature excesses. As I have explained, the temperature excesses are developed according to the structure and





size of the inflorescences, and may be incidental attractants. The temperature excess of the entomophilous Cruciferae are relatively low.

The results of pollination experiments clearly establish the dependence of *Saxifraga oppositifolia*, *Salix arctica*, *Pedicularis arctica* and *P. capitata* on insects for seed set, and the partial dependence of *Dryas integrifolia* on insects for seed set. Diptera are the most important pollinators of all the above except the *Pedicularis* spp. which are pollinated by bumblebees. Bumblebees are important pollinators of them all. All the plants which are dependent, entirely or in part, on insects, particularly Diptera, are highly entomophilous. The only highly entomophilous inflorescence not included is *Arnica alpina* upon which I did not experiment. There are significant differences in the seed set of *D. integrifolia* growing in different regions of the Hazen Camp study area. Plants growing close to sedgy areas along streams and around ponds produce the most seeds, while other areas, particularly if dry or gravelly, produce fewer. This reflects the availability and abundance of pollinators, and the suitability of the different regions to them. Most, if not all, the other flowers around Hazen Camp, are autogamic, viviparous, or anemophilous. Among the dioecious insect pollinated plants, chromosome numbers are low: *S. oppositifolia*  $2N = 26$  (sometimes 39 or 52), *D. integrifolia*  $2N=18$ , *P. arctica*  $2N=16$ , *P. capitata*  $2N = 16$ , perhaps indicating that natural incompatibility mechanisms are still operating (cf. Mosquin, 1966; Gustavson, 1948) such as is expected of plants requiring cross-pollination, I do not discount the possibility of other regions having different races, chromosomal or otherwise, of these plants which do not require cross-pollination.



From the foregoing pages of discussion and conclusions it is obvious that many of the dicotyledons around Hazen Camp display all the attributes of entomophily: they offer visual, olfactory, and other attractants, provide ample food, both solid and liquid upon which many of the insects depend, and offer shelter and warmth. Many plants may have little or no use for insects. However, insects must be responsible for much outcrossing, helping gene flow and population diversity in these plants (Bliss, 1962). Plants with flowers of the highest degrees of entomophily are dependent on insects for seed set, either totally or partially.

Thus these relationships are of utmost importance in biogeographical studies. The paucity of flowers on the northwestern Queen Elizabeth Islands, particularly Ellef Ringnes Island, would definitely prohibit the occurrence of insects (*cf.* McAlpine, 1965), but the lack of insects cannot account for the lack of some flowers, e.g. *D. integrifolia* with its wind dispersed seeds; *Salix arctica* also has plumed seeds and grows on the northwestern Queen Elizabeth Islands. The biogeography of some *Pedicularis* spp. may well be influenced by the occurrence of bumblebees, and *vice versa* as is postulated for the co-distribution of legumes and bumblebees (Panfilov *et al.*, 1960) and other plants and bees (Cockerell, 1932a, b). Those arctic plants apparently restricted because of their pollinators do not have seeds well adapted for long overland dispersal.



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APPENDIX I

THE HAZEN FLORA IN RELATION TO POLLINATION



Key to Symbols, etc.

Species name: collections, P = at Hazen Camp (Powell, 1961)  
S = at Hazen Camp (Savile, 1964)  
T = at Tanquary Fiord (Brassard and Beschel, 1968)  
B & L = at Hazen Camp (Brassard and Longton, 1969)

Insect colour: Human colour:  
(name of colour, symbol as per table 15 and figures 36 and 37)

Insect saturation: Human saturation:  
(per cent colour saturation, wavelength)

Size: UOL: BOL:  
UOL = unbroken outline length  
BOL = total outline length  
(length in cm, classes per table 16)

Movement: Class as per V.6.1.

Form: As per table 18

Figure numeral: As per table 18

Honey guides: Odours: Strength Class as per table 19, Quality:

Convection:

Pollen availability:

Nectar: Amount: as per table 23 Availability: comment on nectary position and ease of access by insects to nectar

Microclimate: Mode of generation as per table 25

Pollination: Mode Entomophily: rating as per table 38

General biology: References by numbers in parentheses

Remarks:  
(R1), (R2), etc. See Remarks 1, 2 etc. Numbers in parentheses, see References.



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Salix arctica Pall.

PST

Insect colour: G, red-pink +  
grey (R1)  
A, green + grey  
(R2, R3)

Human colour: L, yellow + grey (R1)  
J, red-purple + grey  
(R2, R3)

Insect saturation: 65% (R1)  
10% (R2)

Human saturation: 70% (R1)  
20% (R2)

Size: UOL: ca. 8.5 cm, 5 BOL: great, indeterminate, 5

Movement: 2, flickering Form: rhopalomorphic

Odours: (18, 9) Strength: 3 Quality: Sweet

Pollen availability: great quantities, accessible (R1)

Nectar: Amount: abundant (2) Availability: hidden, but easily  
accessible

Microclimate: hairy heat trap Pollination: insect dependent (7,18)

Entomophily: 1 Biology: (7, 9, 18, 25)

Remarks: (R1) staminate catkins, grey is pubescence  
(R2) pistillate catkins, grey is pubescence  
(R3) colours very dull, difficult to determine  
(R4) insects cannot help but become dusted with pollen (R1, 7)

Oxyria digyna (L.) Hill

PST

Insect colour: Human colour: red-green

Pollen availability: abundant Nectar: Amount: nil (9)

Pollination: anemophilous (3, 15) Entomophily: 6

Polygonum viviparum L.

PST

Insect colour: B, yellow

Human colour: W, white

Insect saturation: 70%

Human saturation: 70%

Size: UOL:

BOL: great- indeterminate

Movement: 2, flickering

Form: rhopalomorphic



Odours: (3, 4, 18) Strength: 1 Quality: Sweet

Pollen availability: little (cf. 15) Nectar: (18,9) Amount: some (R2)

Availability: open

Pollination: independent (R1)

Entomophily: 2

Biology: (15, 22, 25)

Remarks: (R1) flowers mostly sterile, viable achenes rare (15, 22)  
(R2) whole inflorescence considered

*Stellaria longipes* Goldie s. lat. (R1, 9) PST

Insect colour: B, yellow

Human colour: W, white

Insect saturation: 85%

Human saturation: 85%

Size: UOL: 3.4 cm, 3

BOL: 4.7 cm, 3

Movement: 1, immobile (R2)

Form: pleomorphic

Figure numeral: 10 (R3)

Honey guides: structural, whole petals

Odours: (3, 9, 18) Strength: 1 Quality: Sweet

Pollen availability: present, but not abundant (31)

Nectar: (3, 8, 9, 15, 31) Amount: some Availability: open (R4)

Pollination: independent (R5) Entomophily: 2

Biology: (3, 4, 22, 25)

Remarks: (R1) four forms P, four species and one hybrid S  
(R2) flowers very low growing and in sheltered places  
(R3) five very deeply indented petals  
(R4) nectaries on receptacle between bases of stamens  
(R5) rarely produces mature seeds (22)



Cerastium alpinum L.

PST

Insect colour: B, yellow (R1)

Human colour: W, white

Insect saturation: 70%

Human saturation: 70%

Size: UOL: 4.2 cm, 3

BOL: 6.1 cm, 4

Movement: 3, mobile

Form: pleomorphic, weakly stereomorphic

Figure numeral: 10 (R2)

Honey guides: 2 translucent lines on each petal

Odours: (3, 9, 18) Strength: 3 Quality: sweet

Convection: possible

Pollen availability: present, not abundant (31)

Nectar: (8, 9) Amount: plenty

Availability: open (R3)

Microclimate: inverted bell

Pollination: independent, self (31)  
insect likely (31)

Entomophily: 3

Biology: (3, 25, 31)

Remarks: (R1) slight ultraviolet reflection (5%) on distal part of petals  
(R2) five petals, each indented  
(R3) nectaries at base of stamens

Cerastium Beeringianum Cham. & Schlecht

PST (R1)

Odours: Strength: 0

Entomophily: 6

Biology: (25)

Remarks: (R1) locally common in wet areas; resembles *C. alpinum* and *C. arcticum*, but is smaller.

Cerastium arcticum Lge

PST

Insect colour: B, yellow (R1)

Human colour: W, white

Insect saturation: 70%

Human saturation: 70%

Size: UOL: -, 3

BOL: -, 3 or 4



Movement: 3, mobile

Form: pleomorphic, weakly stereomorphic

Figure numeral: 10 (R2)

Honey guides: 2, translucent lines on each petal

Odours: Strength: 2

Quality: sweet

Convection: possible

Pollen availability: little

Nectar: Amount: little (9)

Availability: open (R3)

Microclimate: inverted bell

Pollination: independent

Entomophily: 5

Biology (25)

Remarks: (R1, R2, R3) as for *C. alpinum*

*Arenaria* (= *Minuartia*) *rubella* (Wahlenb.) Sm. PST

Insect colour: B, yellow

Human colour: W, white (R1)

Size: UOL: 0.7 cm, 1

BOL: 0.7 cm, 1

Movement: 1, stationary

Form: pleomorphic, weakly stereomorphous (1.9 mm deep)

Figure numeral: 5      Odours: (9)      Strength: 3      Quality: sweet

Pollen availability: very little, if any

Nectar: Amount: little (R2)

Availability: open

Microclimate: probably negligible

Pollination: independent

Entomophily: 6

Biology: (25)

Remarks: (R1) petals mostly hidden by long sepals

(R2) secreted at bases of stamens, where it is visible as sparkling droplets

*Arenaria Rossii* R. Br.

PST (R1)

Remarks: (R1) similar to *A. rubella*. Rare at Hazen Camp (25) although common elsewhere in arctic archipelago (22)





Silene acaulis L. var. exscapa (All.) DC

PST

Insect colour: (R1)

Human colour: (R1)

Insect saturation: (R1)

Human saturation: (R1)

Size: (3) UOL: 3 cm, 3

BOL: 5.5 cm, 4

Movement: stationary

Form: stereomorphic, secondarily amorphic (R2)

Figure numeral: 5

Honey guides: none detected

Odours: (3, 4,9, 31) Strength: 2 Quality: sweet (R3)

Pollen availability: some, not abundant (R4)

Nectar: Amount: plenty (9)

Availability: only to insects with proboscides (R5)

Pollination: probably independent (R6)

Entomophily: at least 5 (R6)

Biology: (3, 4, 31)

Remarks: (R1) not examined: see *Saxifraga oppositifolia*, *Erysimum Pallasii* and *Epilobium latifolium*.

(R2) flowers in mats

(R3) reported similar to *Melandrium* spp. (15)

(R4) may or may not be present (31), used by bees (10)

(R5) secretion base of stamens and possibly base of ovary (31)

(R6) evidence for cross-pollination (31). Rare around Hazen Camp (25) and so not studied. Common elsewhere (22)

*Melandrium (= Lychnis) apetalum* (L.) Fenzl. ssp. *arcticum* (Fr.) Hult. PST

Insect colour: blue-green-grey

Human colour: purple (R1)

Insect saturation: 10%

Human saturation: 10%

Size: UOL: (R1)

BOL: (R1)

Movement: 4, mobile

Form: stereomorphic, 1.3 cm deep

Figure numeral: 5 (R1)

Honey guides: none detected (R1)

Odours: Strength: 3 (R2)

Quality: bittersweet (R2)

Pollen availability: present, but not abundant



Nectar: Amount: some, but not plenty Availability: only to insects with long proboscides, or very small insects

Microclimate: microgreenhouse Pollination: independent

Entomophily: 6 Biology: (15, 31)

Remarks: (R1) petals not always exerted from syncalyx; if exerted diameter less than 0.5 cm. syncalyx bulb diameter 1.1 cm

Melandrium (=Lychnis) affine (J. Vahl) Hartin. PT (R1, R2)

Entomophily: 6 Biology: (31)

Remarks: (R1) also referred to as *M. furcatum* (Raf.) Hult.; *M. involucratum* Cham. & Schlecht; similarly under gn. *Lychnis*; and *Wahlbergella affinis* Fries.  
(R2) not distinguished from *M. triflorum*, see *M. triflorum*

Melandrium triflorum (R.Br.) J. Vahl

Insect colour: B, yellow Human colour: W, white

Insect saturation: 70% Human saturation: 70%

Size: UOL: 4.5 cm, 3 BOL: 6.0 cm, 4

Movement: 4, swaying Form: stereomorphic

Figure numeral: 5, secondarily 10 (R1)

Honey guides: none detected

Odours: (9, 28, 31) Strength: 3 Quality: bittersweet (R2)

Pollen availability: plenty

Nectar: Amount: plenty Availability: only to insects with long proboscides, or small insects

Microclimate: microgreenhouse Pollination: independent (R3)



Entomophily: 6

Biology: (31)

Remarks: (R1) petals not deeply indented as *S. longipes* and *Cerastium* spp.  
(R2) typical of campion, nectar so flavored (9)  
(R3) self-pollination inevitable (31)

*Ranunculus hyperboreus* Rottb. PST

*R. trichophyllus* Chaix. var. *eradicatus* (Laest.) W.B. Drew PS

*R. subrigidus* W. B. Drew B&L

Insect colour: dull-red

Human colour: dull-yellow

Size: UOL: -, 1

BOL: -, 1

Movement: 1, stationary (R1)

Form: pleomorphic

Figure numeral: 5

Pollination: independent (R2)

Biology: *R. hyperboreus* (13, 27) Entomophily: 6

Remarks: (R1) amphibious plants, flowers lie on wet mud, sometimes under water  
(R2) cleistogamous (27), also vegetative reproduction

*Ranunculus pedatifidus* Sm. var. *leiocarpus* (Trantv.) Fern. PT B&L (R1)

Insect colour: (R1)

Human colour: B, yellow

Size: UOL: -, 2

BOL: -, 2

Form: pleomorphic

Figure numeral: 5

Honey guides: unknown (R1)

Biology: (14) as *R. affinis*

Remarks: (R1) rare in study area  
(R2) possibly C+J, red + red-purple; or C, red  
see *R. sulphureus*





Ranunculus Sabinei R. Br.

PT

Insect colour: (R1)

Human colour: B, yellow

Size: UOL: -, 2 or 3

BOL: -, 2 or 3

Form: pleomorphic

Figure numeral: 5

Honey guides: (R1)

Biology: (16, 7)

Remarks: (R1) possibly C+J, red + red-purple; or C, red; see  
*R. sulphureus*

Ranunculus sulphureus Sol.

Insect colour: C+J, red + red-purple (R1)

Human colour: B, yellow

Insect saturation: 65%

Human saturation: 65%

Size: (3) UOL: -, 3

BOL: -, 4

Movement: 1, stiff

Form: pleomorphic

Figure numeral: 5

Honey guides: none detected

Odours: (18, 4) Strength: 0 (R2) Convection: probable

Pollen availability: present

Nectar: Amount: unknown

Availability: nectaries present (13)

Microclimate: parabolic reflector Pollination: (R3)

Entomophily: 6

Biology: (13, 25)

Remarks: (R1) red-purple distally on petals  
(R2) slight scent reported by (4)  
(R3) self pollination difficult, gynoecium overtops androecium,  
anthers extrorse(13)



Papaver radicatum Rottb.

PST

Insect colour: C, red

Human colour: B, yellow

Insect saturation: 85%

Human saturation: 85%

Size: UOL: 7.1, 4

BOL: 7.1, 4

Movement: 4, swaying

Form: pleomorphic (weakly stereomorphic, fully open)

Figure numeral: 4 (R1)

Honey guides: nil

Odours: Strength: 2 (R2)

Quality: of poppy

Convection: yes

Pollen availability: abundant (R3)

Nectar: Amount: nil (9) (R3)

Availability:

Microclimate: parabolic reflector

Pollination: independent

Entomophily: 2

Biology: (3, 4, 15, 25)

Remarks: (R1) petals overlap, figure numeral not pronounced  
(R2) absent (18, 9) faint (3, 4)  
(R3) *Papaver* spp. classified as pollen flowers (6)

Cochlearia officinalis L.

S (R1) T

Eutrema Edwardsii R. Br.

PST

Cordamine bellidifolia L.

PST

C. pratensis L. var. angustifolia Hook. (R2)

PST

Halimolobos mollis (Hook.) Rollins

P

Insect colour: B, yellow (R3)

Human colour: W, white

Insect saturation: 65%

Human saturation: 65% (R3)

Size: UOL: -, 1

BOL: -, 1

Movement: 1, stiff

Form: pleomorphic, weak to medium stereomorphic



Figure numeral: 4

Honey guides: none detected

Odours: (3)      Strength: 0

Pollen availability: some

Nectar:(3) Amount: nil

Pollination: independent

Entomophily: 6

Biology: (3, 4, 15, 22)

Remarks: (R1) single plant (25), flowers not examined

(R2) purely vegetative at Hazen Camp (25), blooms elsewhere  
(3, 22)

(R3) *Eutrema Edwardsii* only; others probably, but not examined

*Lesquerella arctica* (Wormskj.) Watson

Insect colour: C, red

Human colour: B, yellow

Insect saturation: 65%

Human saturation: 65%

Size: UOL: 3.4, 2

BOL: 6.8 , 3

Movement: 1, stiff

Form: pleomorphic, weakly stereomorph (0.37 cm deep)

Figure numeral: 4

Honey guides: none detected

Odours: (9)      Strength: 3

Quality: sweet

Pollen availability: plenty (R1)

Nectar: Amount: plenty Availability: open

Microclimate: inverted bell (R2)

Pollination: independent

Entomophily: 2

Biology: (25)

Remarks: (R1) in a few flowers very little is available

(R2) flowers close slightly in cloudy weather

*Draba alpina* L.

P (R1)

*D. Bellii* Holm.

PST

Insect colour: C, red

Human colour: B, yellow

Insect saturation: 65%

Human saturation: 65%



Size: UOL: 2.6 cm, 2 (R2)

BOL: 2.6 cm, 2 (R2)

Movement: 1, stiff

Form: secondarily amorphic to rhopalomorphic inflorescence; flowers medium stereomorphic (0.4 cm deep, tube entrance 0.4 x 0.3 cm)

Figure numeral: 4(R2)

Honey guides: none detected

Odours: Strength: 2

Quality: sweet

Pollen availability: some

Nectar: Amount: some

Availability: available to most insects (see form)

Microclimate: possible, inverted bell

Pollination: independent

Entomophily: 2

Remarks: (R1) not examined: may grow outside study area in stream beds above 300 m.

(R2) are really in large class 5, see form.

<u><i>Draba nivalis</i> Liljeb1.</u>	<u>P</u>
<u><i>D. lactea</i> Adams</u>	<u>PST</u>
<u><i>D. subcapitata</i> R. Br.</u>	<u>PST</u>
<u><i>D. oblongata</i></u>	<u>PST</u>
<u><i>D. cinerea</i></u>	<u>PST</u>
<u><i>D. groenlandica</i></u>	<u>PST</u>

Insect colour: B, yellow

Human colour: W, white

Insect saturation: 65%

Human saturation: 65%

Size: UOL: 1.8 - 2.7 cm, 1-2

BOL: 1.8 - 2.7 cm, 1-2

Movement: 1-2, stiff to mobile stiff

Form: see *D. Bellii*

Figure numeral: 4

Odours: Strength: 0

Pollen availability: little to some

Nectar: Amount: nil to little

Availability: see form





Microclimate: possible, inverted bells (R1)

Pollination: independent

Entomophily: 6

Remarks: (R1) temperature excesses in *D. groenlandica* negligible

*Erysimum Pallasii* (Pursh) Fern.

Insect colour: A, green

Human colour: F, purple

Insect saturation: 45%

Human saturation: 65%

Size: UOL: 4.6 cm, 3

BOL: 6.6 cm, 3

Movement: 2, mobile stiff

Form: stereomorphic (0.85 cm deep, tube entrance diameter 0.3 cm), rhopalomorphic (R1)

Figure numeral: 4 (R2)

Honey guides: none detected

Odours: Strength: 4 (R3)

Quality: sweet

Pollen availability: plenty

Nectar: Amount: plenty (9)

Availability: only to long tongued insects; see form (R4)

Microclimate: yes

Pollination: independent

Entomophily: 3

Biology (25)

Remarks: (R1) many flowers in juxtaposition on raceme  
(R2) flowers not circular in plan, petals form 'X'.  
(R3) recorded as scented (9, 22), scentless (18)  
(R4) secreted at bases of short stamens

*Braya humilis* (C.A. Mey.) Robins ssp. *arctica* (Böcher) Rollins PST (R1)

Insect colour: B, yellow (R2)

Human colour: W, white (R2)

Insect saturation: 65%

Human saturation: 65%

Size: UOL: 2.2 cm, 2

BOL: 3.3 cm, 3 (R3)

Movement: 2, mobile stiff

Form: pleomorphic, weakly stereomorphic (0.3 cm deep, tube entrance diameter 0.2 x 0.3 cm) (R3)



Figure numeral: 4 (R4)

Honey guides: none detected

Odours: Strength: 1

Quality: sweet

Pollen availability: some

Nectar: Amount: little (9)

Availability: not readily visible,  
but not out of reach  
of most insects.

Microclimate: yes

Pollination: independent

Entomophily: 5

Biology: growing luxuriantly on  
landing strip N11 (see  
Fig. 3) (25)

Remarks: (R1) subspecific name not used by (25)  
(R2) some flowers tinged with purple, insect-blue-green.  
(R3) inflorescence loose raceme, ?secondarily amorphic,  
size medium-large, 4  
(R4) petals form 'X'

*Braya purpurescens* (R.Br.) Bunge PST

*B. Thorild-Wulfii* Ostenf.-Low PST

Insect colour: B, yellow

Human colour: W, white

Insect saturation: 65%

Human saturation: 65%

Size: UOL: 1.5 cm, 1

BOL: 1.5 cm, 1 (R1)

Movement: 1, stiff

Form: weakly stereomorphic (0.3 cm  
deep, entrance diameter 0.2 cm)

Figure numeral: 4 (R2)

Honey guides: none detected

Odours: Strength: 0

Pollen availability: some

Nectar: Amount: very little (9) (R3)

Pollination: independent (cf. 15) Entomophily: 5

Remarks: (R1) loosely capitate inflorescence, ? class 3  
(R2) petals overlap, flowers with circular outline  
(R3) I could find no nectar



<u>Saxifraga nivalis</u> L.	<u>PST</u> (R1)
<u>S. foliolosa</u> R. Br.	<u>PST</u> (R1)
<u>S. rivularis</u> L. s. lat.	<u>PS</u> (R1)
<u>S. tenuis</u> Sm.	<u>PST</u> (R1)

Insect colour: B, yellow (R2)      Human colour: W, white  
Size: UOL: -, 1      BOL: -, 1  
Figure numeral: 5      Pollination: independent  
Entomophily: 6      Biology (3, 4, 22)  
Remarks: (R1) *S. nivalis* only one of these from dry habitats

Saxifraga caespitosa L. s. lat.      ST P

S. caespitosa ssp. uniflora (R.Br.) Porsild (Ch.)      T

S. caespitosa ssp. exaratooides (Simm.) Engl. & Irmsch. emend Porsild (Ch.)

(vide 20, 22)      P

Insect colour: D, orange      Human colour: L, pale yellow  
Size: UOL: -, 2      BOL: -, 3  
Movement: 2, mobile stiff      Form: pleomorphic  
Figure numeral: 5      Odours: Strength: 0 (R1)  
Pollen availability: little      Nectar: Amount: nil (R2)      Availability: R(9)  
Entomophily: 6  
Remarks: (R1) scented (3) not scented (4)  
(R2) present and exposed (15); flowers generally solitary,  
rarely 2 per scape, if so second is reduced (2)





Saxifraga cernua L.

PST

Insect colour: B, yellow (R1)

Human colour: W, white (R1)

Size: UOL: -, 3

BOL: -, 4

Movement: 3, mobile

Form: pleomorphic

Figure numeral: 5

Honey guides: (R1)

Odours: Strength: 1

Quality: (R2)

Pollen availability: little Nectar: Amount: little Availability: open

Microclimate: inverted bell, not measured

Pollination: probably independent Entomophily: 6  
(R3)

Remarks: (R1) the bases of petals of some flowers are marked in  
red (insect-black), especially on veins  
(R2) of almonds (3, 4)  
(R3) reproduction through bulblets

Saxifraga flagellaris Wild. ssp. platysepala (Trautv.) Porsild PST

Insect colour: C, red

Human colour: B, yellow

Insect saturation: probably 65%

Human saturation: probably 65% + (R1)

Size: UOL: -, 3

BOL: -, 3

Movement: 2, mobile stiff

Form: pleomorphic

Figure numeral: 5

Honey guides: none detected

Odours: Strength: 1

Pollen availability: little

Nectar: Amount: nil (R2)

Availability: open

Microclimate: inverted bell (R1) Pollination: probably independent (R3)

Entomophily: 6

Remarks: (R1) not measured  
(R2) little under experimental conditions (9)  
(R3) reproduction vegetative through bulblets



Saxifraga Hirculus L. var. propinqua (R.Br.) Simm.      PST

Insect colour: C + E (R1)      Human colour: B+D, yellow + orange (R1)  
Size: UOL: 3.5, 3      BOL: 5.2, 4  
Movement: 2, mobile stiff      Form: pleomorphic  
Figure numeral: 5      Honey guides: (R1)  
Odours: Strength: 2 (R2)      Quality: sweet  
Pollen availability: little      Nectar: Amount: little (9)      Availability: open (R4)  
Microclimate: inverted bell (R3)      Pollination: probably independent  
Entomophily: 3  
Remarks: (R1) each petal yellow with orange spots; to insects petals distally insect-purple, proximally insect-red with insect-dark-red spots and 2 insect-purple spots corresponding to basal swelling.  
(R2) as scentless (34)  
(R3) not measured  
(R4) secreted around hypanthium (4)

Saxifraga oppositifolia L.      PST

Insect colour: M, yellow-green      Human colour: E, purple (R1)  
Insect saturation: 43%      Human saturation: 43%  
Size: UOL: 3.7 cm, 3      BOL: 5.5 cm, 4  
Movement: 2, mobile stiff      Form: secondarily amorphic, pleomorphic  
Figure numeral: 5      Honey guides: none detected  
Odours: (R2) Strength: 3      Quality: sweet  
Convection: yes      Pollen availability: abundant (R1)  
Nectar: Amount: abundant      Availability: open  
Microclimate: inverted bell      Pollination: dependent      Entomophily: 1  
Remarks: (R1) pollen bright yellow (insect-red)  
(R2) none (18,30), slight (4), strong (3, 11), present (19)



Saxifraga tricuspidata Rottb.

Insect colour: D + Blk, orange  
+ black spots

Human colour: L+C, pale yellow +  
red spots

Insect saturation: 65%

Human saturation: 65%

Size: UOL: 3.5, 3

BOL: 3.5, 3

Movement: 3, mobile

Form: pleomorphic

Figure numeral: 5

Honey guides: spots (see text)

Odours: Strength: 2 (R1)

Quality: sweet

Pollen availability: some

Nectar: Amount: plenty (R2)

Availability: open (R2)

Pollination: independent

Entomophily: 3

Remarks: (R1) scentless (18)

(R2) much more nectar present in flowers under insect excluders  
(cf. pollination in text) secreted at bases of ovaries  
and filaments

Potentilla nivea L. spp. Chamissonis (Hult.) Hiit PT (R1)

as P. Chamissonis Hult. S

P. rubricaulis Lehm. PST (R1)

Insect colour: C, red

Human colour: B, yellow

Insect saturation: 85%

Human saturation: 85%

Size: UOL: 3.6 cm, 3

BOL: 5.4 cm, 4

Movement: 4, swaying

Form: pleomorphic

Figure numeral: 5 (secondarily 10, but weak, each petal slightly indented)

Odours: Strength: 2

Quality: sweet

Convection: yes

Pollen availability: plenty

Nectar: Amount: plenty (8,9,25,32) Availability: open

Microclimate: parabolic reflector Pollination: independent (14)

Entomophily: 1

Biology: (14)











Pollination: partially independent

Entomophily: 1

Biology: (R4) (9, 14, 25)

Remarks: (R1) affinities with *D. octopetala* L. etc. discussed by ( ,  
(R2) two tone effect, indeterminate extra length, varying  
with age of flower -- class 5  
(R3) secreted on inner site of hypanthium between gynoecium  
and androecium, space about 1 mm across. Nectar lies  
about 0.5 cm below stigmas  
(R4) selfing easy (14)

*Epilobium latifolium* L.

PST

Insect colour: H+Q, bright green + dull blue-green  
(R1) Human colour: E, purple

Insect saturation: 55%

Human saturation: 65%

Size: UOL: 10.1 cm, 5

BOL: 20.2 cm, 5

Movement: 3, mobile

Form: pleomorphic

Figure numeral: 8

Honey guides: probably none (R1)

Odours: Strength: 1

Pollen availability: abundant, but  
grains held  
together with  
strands of viscin

Nectar: Amount: abundant

Availability: hidden between bases of  
filaments, tube so formed  
about 0.3 cm deep

Pollination: independent

Entomophily: 3

Biology: (15)

Remarks: (R1) dull blue-green veins

*Epilobium arcticum* Samuelss. P

as *E. davuricum* Fisch. var. *arcticum* (Samuels) Polunin S (R1)

Remarks: (R1) not examined, rare: flowers small and inconspicuous



Hippurus vulgaris L.      PST   (R1)

Remarks: (R1) few small inconspicuous flowers in axils of uppermost leaves (22); probably vegetative reproduction, but possibly anemophilous also (15, 26)

Cassiope tetragona (L.) D. Don      PST

Insect colour: B, yellow.

Human colour: W, white

Insect saturation: 65%

Human saturation: 65%

Size: UOL: 2.2 cm, 2

BOL: 2.2 cm, 2

Movement: 2, mobile stiff

Form: stereomorphic, but open

Figure numeral: pentamerous synpetalous corolla, no number to insects

Honey guides: none detected

Odours: Strength: 1

Quality: sweetly aromatic (R1)

Pollen availability: some, grains in tetrads

Nectar: Amount: little

Availability: hidden as flowers open downwards

Microclimate: hanging bell

Pollination: independent (R2)

Entomophily: 5

Biology: (29)

Remarks: (R1) faint (22), sweet aromatic (9), like Lily of the Valley but not powerful (29); absent (18)

(R2) see also (29) for adaptations to insects, possibility of selfing, and cleistogamy

Androsace septentrionalis L.      PST   (R1)

Insect colour: B, yellow (R2)

Human colour: W, white

Size: UOL: -, 1

BOL: -, 1

Form: pleomorphic, weakly stereomorphic

Figure numeral: 5



Nectar: Amount: little (9)      Biology: (16)

Remarks: (R1) scarce (25)  
(R2) probable, flowers not examined

Armeria maritima (Mill.) Willd. ssp. labradorica (Wallr.) Hult. TB&L (R1)

Remarks: (R1) one plant collected in 1967

Pedicularis capitata Adams

Insect colour: P+D, pink-orange      Human colour: L, pale yellow  
+ orange

Insect saturation: 65%      Human saturation: 65%

Size: UOL:      BOL: -, 4 (R1)

Movement: 2, mobile stiff      Form: zygomorphic (R1) (tube 1.23  
cm deep)

Honey guides: convolutions on corolla lip

Odours: Strength: 0 (22)      Pollen availability: plenty, for  
Bombus only

Nectar: Amount: abundant      Availability: only to insects with  
long proboscides, or  
small insects

Microclimate: microgreenhouse      Pollination: Bombus dependent

Entomophily: 4

Remarks: (R1) 2-5 flowers per inflorescence

Pedicularis arctica R. Br.      ST (R1)

Insect colour: N, pale yellow-  
green      Human colour: 9, red-pink

Insect saturation: 55%      Human saturation: 85%





Size: -, 4 (see form)                      Movement: 1, stiff  
Form: zygomorphic (tube 1.2 cm deep), rhopalomorphic                      Honey guides: convolutions on corolla lip  
Odours: (18)    Strength: 1                      Quality: sweet  
Pollen availability: plenty, for *Bombus* only  
Nectar: Amount: abundant (9)                      Availability: only to insects with long proboscides, or small insects  
Microclimate: microgreenhouse                      Pollination: *Bombus* dependent  
Entomophily: 2 (R2)  
Remarks: (R1) *Pedicularis* sp. recorded by (23). Affinities to *P. hirsuta* and *P. langsдорffi* Fisch. ex Steven in (20, 25)  
                    (R2) also (4)

*Pedicularis hirsuta* L.                      PST    (R1)    (R2)

Form: zygomorphic (tube 0.9 cm deep), rhopalomorphic  
Odours: (3, 4)    Strength: 0                      Pollination: ?  
Entomophily: 4  
Remarks: (R1) see (R1) in *P. arctica* and (20, 25)  
                    (R2) similar to *P. arctica*; references to *P. hirsuta* (1, 3, 4, 9, 17, 20, 25)

*Pedicularis sudetica* Willd.                      ST    (R1)

Remarks: (R1) rare in study area, not examined: probably similar to *P. arctica*. References on (3, 8, 9, 17, 18, 25)

*Erigeron compositus* Pursh var. *discoideus* Gray                      PST

Insect colour: B+C, yellow + red                      Human colour: W+B, white + yellow  
Insect saturation: 70%                      Human saturation: 70%  
Size: UOL: 5.8 cm, 4                      BOL: 17.4 cm, 5



Movement: 2, mobile stiff

Form: zygomorphic, secondarily actino-  
morphic (disc florets 0.1 cm  
deep ) (R1)

Honey guides: none detected

Odours: Strength: 2 (R2) Quality: of daisy

Convection: yes

Pollen availability: some

Nectar: Amount: little (R3)

Availability: see form

Microclimate: disc

Pollination: probably independent

Entomophily: 4

Remarks: (R1) 33-41 ray florets  
(R2) scentless (18)  
(R3) none (9)

*Erigeron eriocephalus* J. Vahl. PS (R1)

Insect colour: B+C, yellow +  
red

Human colour: W+K, white + orange

Insect saturation: 65%

Human saturation: 65%

Odours: Strength: 1

Quality: of daisy

Pollination: probably independent Entomophily: 6

Remarks: (R1) similar to *E. compositus*, ray florets smaller and  
tend to blend with grey villous involucre

*Antennaria Ekmaniana* Porsild P (R1)

Remarks: (R1) not found

*Chrysanthemum integrifolium* Richards PT (R1)

Insect saturation: 65%

Human saturation: 65%

Nectar: not examined

Pollination: probably independent







Nectar: Amount: little      Microclimate: disc

Pollination: independent      Entomophily: 2

Remarks: (R1) not listed in (22, 23) but most common *Taraxacum* in study area (25)

*Taraxacum hyparcticum* Dahlst.      PS      (R1)

*T. pumilum* Dahlst.      PST      (R1)

*T. phymatocarpum* J. Vahl.      PST      (R1)

Remarks: (R1) all 3 species occasional (25), scentless (18), no pollen in *P. hyparcticum* (22), florets tinged with pink in *P. hyparcticum*, inflorescence of *P. phymatocarpum* does not fully open (22), ultraviolet reflections unknown: other references (3, 4, 18)





APPENDIX II

Inflorescences and Their Visitors, Numbers of Each, and Purpose of  
Their Visits (Based on 1967 Collection)

Key to Symbols:

I = immature

M = males

F = females

U = sex undetermined

A = in ambush

A' = in ambush with prey; or being eaten

B = basking

C = copulating

N = feeding on nectar

O = feeding on ovarian and other attached tissues

P = taking pollen for food

Q = undetermined activity

D = dusted with pollen

E = not dusted with pollen

G = not examined for pollen dusting

R1, R2, etc., see Remarks



## References

- 1 Aurivillius 1883
- 2 Corbet 1964
- 3 Diechman in Hartz 1895
- 4 Downes 1964
- 5 Ekstam 1894 a
- 6 Ekstam 1894 b
- 7 Ekstam 1897
- 8 Ekstam 1899
- 9 Frison 1911
- 10 Hartz 1895
- 11 Hocking 1968
- 12 Hocking and Sharplin 1965
- 13 Høeg 1924
- 14 Høeg 1932
- 15 Høeg 1929
- 16 Holmen 1957
- 17 Holmgren 1869
- 18 Jessen 1913
- 19 Johansen 1921
- 20 Kjellman in Warming (1909) and Ekstam (1897)
- 21 Knuth 1906
- 22 Lindman (1887) in Warming (1909)
- 23 McAlpine 1965
- 24 McLachlan 1879
- 25 Milliron and Oliver 1966
- 26 Mosquin and Martin 1967
- 27 Porsild in Matheisen 1921
- 28 Richards 1970
- 29 Savile 1959
- 30 Savile 1964
- 31 Schneider 1894
- 32 Schneider 1895
- 33 Schneider 1908
- 34 Shamurin 1962
- 35 Shamurin pers. comm.
- 36 Shewell in McAlpine 1965
- 37 Swales 1966
- 38 Warming 1909



*Salix arctica* staminate catkins

<i>Acarina</i>	several U	; QG
<i>Pardosa glacialis</i>	1I	; ?AE
<i>Xysticus deichmanni</i>	2IM, 2F, 2IF	; 1IMAD, 1IMAE, 2FAD, 1IFAD
<i>Byrdia</i> sp.	1I	; OG
Noctuidae	1I	; OG
<i>Anarta richardsoni</i>	1U, 6IU	; 1UQG, 6IUOG
<i>Boloria polaris</i>	2U	; 1NG, 1NE
<i>Tipula arctica</i>	1U	; QD
<i>Limnophyes</i> sp. or spp.	9M, 19F	; 9MQ?CD, 19F?ND
<i>Smittia</i> sp. or spp.	7M, 1F	; 6MQ?CD, 1MQ?CE, 1FQD
<i>Smittia velutina</i>	193F	; 193 FND
Empididae		(1968)
<i>Carposcalis carinata</i>	9M, 4F, 5U	; 7MPD, 1MQ?PD, 1MQG, 3FPD, 1FQ?PD, 5UQG
<i>Phalacrodira nigropilosa</i>	4M, 4F	; 2MPD, 1MA'G, 1MQD, 2FPD, 1FA'G, 1FQD
<i>Metasyrphus chillcotti</i>	1M, 2F	; 1MPD, 2FQ?BD
Calliphoridae	3U	; 2UND, 1UNG
<i>Boreellus atriceps</i>	3F, 5U	; 3FNE, 5UNG
<i>Scatophaga apicaulis</i>	3M, 1F, 2U	; 1MND, 1MA'G, 1MQE, 1FQE, 1UA' & NG, 1UQG
<i>S. multisetosa</i>	1F	; QG
<i>Fucellia pictipennis</i>	2U	; 1NG, 1QD
<i>Eupogonomyia groenlandica</i>	1F	; ND
<i>Nematus</i> sp.	1U	; QE
<i>Parasitica</i>	1U	; QG
<i>Cryptus arcticus</i>	1F	; QE
<i>Oresbius</i> sp.	1U	; QD
<i>Bombus</i> spp.	see text	





*Salix arctica* pistillate catkins

<i>Acarina</i>	4U	; QG
<i>Boloria chariclea</i>	1U	; QG
<i>Plebius aquilo</i>	1U	; QG (catkins in seed)
<i>Chironomidae</i>	1F, 2U	; 1 FQG, 2U?N
<i>Limmophyes</i> sp. or spp.	1M, 18F	; M?CG, 18F?N?CG
<i>Paraphaenocladus despectus</i>	5F	; NG
<i>Smittia</i> sp.	1F	; QG
<i>S. velutina</i>	1F	; NG
<i>Cecidomyiidae</i>	eggs	
<i>Syrphidae</i>	3U	; QG
<i>Carposcalis carinata</i>	1M	; NG
<i>Phalacrodira nigropilosa</i>	1M, 3F	; 1MND, 2FQD, 1FQE
<i>Metasyrphus chillcotti</i>	2F	; QD
<i>Calliphoridae</i>	2U	; NG
<i>Boreellus atriceps</i>	1M, 1F	; 1MNE, 1FNE
<i>Phormia terraenovae</i>	1M	; NE
<i>Pectinarctica stylata</i>	1F	; NE
<i>Periscepsia</i> sp.	1M	; ND (R1)
<i>Scatophaga apicaulis</i>	1F, 2U	; 1FA'G, 2UNG
<i>Fucellia pictipennis</i>	1M	; QD
<i>Nematus</i> sp.	2M, 1F, 2U	; 1MQG, 1FQG, 1UA'G, 1UQD eggs
<i>Bombus</i> spp.	see text	

(R1) also visited flowers of *Saxifraga oppositifolia*

*Salix arctica* undetermined sex

<i>Pardosa glacialis</i>	1I	; ?AE
<i>Boreellus atriceps</i>	2M, 2F	; 2MNE, 2FNE

References: 3, 4, 10, 11, 15, 16, 23, 25, 28

*Oxyria digyna*

<i>Anarta richardsoni</i>	2I	; OG
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*Polygonum viviparum*

<i>Noctuidae</i>	12U	; NG
<i>Anarta richardsoni</i>	1M, 1U	; 1MNE, 1UNG
<i>Crymodes exulis</i>	1M	; NE
<i>Lasiestra leucocycla</i>	1F	; NE
<i>Boloria chariclea</i>	1M, 2U	; 1MNE, 2UNG
<i>Lycaena feildeni</i>	1M	; QE



*Polygonum viviparum* (contd.)

<i>Plebius aquilo</i>	2M, 11U	; 2MNE, 11UNG
<i>Dolichopus dasyops</i>	1M	; NE
<i>Rhamphomyia filicauda</i>	3F	; 3FNE
<i>R. nigrita</i>	3F	; 1FND, 2FNE
<i>Peleteria aenea</i>	4M, 1F	; 2MNE, 1MND, 1MQG, 1FND
<i>Pogonomyoides segnis</i>	1M	; A'E (R1)
<i>Spilogona sanctipauli</i>	1M	; ND

(R1) dead of fungus (*Entomophthora muscae*) disease

References: 11, 21, 28, 32

*Stellaria longipes*

<i>Boloria chariclea</i>	1F	; ND
Chironomidae	1U	; QE
<i>Corynoneura</i> sp.	4M, 8F	; 11?N, 1Q, 1E, 11G
<i>scutellata</i>		
<i>Bradysia</i> sp.	1F	; QE
<i>Dolichopus dasyops</i>	2M	; QE
<i>Peleteria aenea</i>	1M	; ND (R1)
<i>Spilogona melanosoma</i>	1M	; NG
Chalcidae	4U	; 2NE, 2QE
<i>Tridymus</i> sp.	5U	; NG
<i>Atractodes</i> sp.	2M, 2F	; 1MNG, 1MQG, 1FND, 1FNG
<i>Mesoleptus</i> sp.	1F	; NG
<i>Stenomacrus</i> sp.	4M, 15F	; 2MNG, 2MQG, 8FN, 7FQ, 4FD, 4FE, 7FG
<i>Tetrastichus</i> sp.	2U	; NG
<i>Bombus</i> spp.	see text	

References: 7, 8, 10, 28

*Cerastium alpinum*

<i>Colias hecla</i>	2	; NG (1968)
Chironomidae	several	; QG (1968)
Muscidae	several	; QG (1968)
<i>Bombus</i> spp.	see text	

References: 7, 8, 10, 11, 17, 21, 26



*Cerastium arcticum*

Reference: 11

*Silene acaulis*

References: 7, 8, 11, 13, 15, 21, 25, 28, 31, 33

*Melandrium triflorum*

Noctuidae 1 ; NG (1968)

Reference: 28 (under *M. affine*)

*Ranunculus sulphureus*

*Limmophyes* sp. 1M ; QE

References: 7, 8

*Papaver radicum*

<i>Bryobia "praetiosa"</i>	many	; QG
<i>Sympistris labradoris</i>	1M	; N(trying) E
<i>Colias hecla</i>	1U	; Q (R1)
<i>Limmophyes</i> sp. or spp.	3F	; QG
<i>Smittia</i> sp.	1F	; QG
<i>Trissocladius</i>	1M	; QG
<i>Rhamphomyia filicauda</i>	3M, 1F	; 1MB, 2MQ, 2MD, 1ME, 1FQD
<i>Carposcalis carinata</i>	1F	; PG
Muscidae	4U	; QG
<i>Eupogonomyia groenlandica</i>	1F	; N(trying) D
<i>Spilogona sanctipauli</i>	2M	; 1BD, 1QE
<i>Bombus polaris</i>	see text	

References: 7, 8, 11, 12(R2), 25, 28

(R1) landed for 8 seconds

(R2) not substantiated by 11



*Lesquerella arctica*

<i>Bryobia "praetiosa"</i>	many U	; QG (R1)
<i>Dictyna borealis</i>	1U	; QG
<i>Entomobrya comparata</i>	20U	; 15 P, 5Q
<i>Heterotrissocladius subpilosus</i>	1M	; QG
<i>Smittia</i> sp. or spp.	2F	; ?BE
<i>Bradysia</i> sp. or spp.	6F	; 4ND, 2NE
<i>Rhamphomyia</i> sp.	1U	; N
<i>R. filicauda</i>	1F	; BE
<i>Carposcalis carinata</i>	1F	; Q?P (R2) D
<i>Peleteria aenea</i>	1F	; N or PD (R3)

References: 11, 23

(R1) also over other parts of plants

(R2) some possibly N

(R3) visited several flowers

*Draba* spp.

<i>Bryobia "praetiosa"</i>	many U	; QG (R1)
<i>Protanypus caudatus</i>	1F	; QG
<i>Eupogonomyia groenlandica</i>	1F	; QE

Reference: 11

(R1) also over other parts of plants

*Draba alpina*

Reference: 8

*Draba Bellii*

<i>Bryobia "praetiosa"</i>	many U	; QG (R1)
<i>Chironomidae</i>	few	1968
<i>Bradysia</i> sp. or spp.	several	; N 1968

Reference: 11

(R1) also over other parts of plants





*Draba cinerea*

*Bryobia "praetiosa"*                      several                      ; QG (R1)

Reference: 11

(R1) also over other parts of plants

*Draba groenlandica*

*Bryobia "praetiosa"*                      several                      ; QG (R1)  
*Syrphidae*                                      1Q                                      ; PG 1968

(R1) also over other parts of plants

*Erysimum Pallasii*

*Bryobia "praetiosa"*                      many                                      ; QG (R1)  
*Xysticus deichmanni*                      1I                                      ; AE  
*Carposcalis carinata*                      1M, 1F                                      ; 2PE

References: 11, 23

(R1) also over other parts of plants

*Braya spp.*

*Bryobia "praetiosa"*                      many                                      ; QG (R1)

Reference: 11

(R1) also over other parts of plants

*Braya purpurescens*

*Bryobia "praetiosa"*                      many                                      ; QG (R1)

Reference: 13

(R1) also over other parts of plants

*Saxifraga caespitosa*

References: 7, 8, 17



*Saxifraga cernua*

References: 7, 8, 11

*Saxifraga flagellaris*

Reference: 11

*Saxifraga Hirculus*

Nematocera	1F	; NE
Chalcidae	1U	; QG
<i>Stenomacrus</i> sp.	1M, 1U	; MQG, UPG

References: 7, 8, 11, 20, 13

*Saxifraga nivalis*

References: 7, 8

*Saxifraga oppositifolia*

<i>Arctoseius cetratus</i>	10F	; ?AG
Eriophyidae	2F	; ?OG
<i>Cecidophyes</i> sp.	2F	; ?OG
<i>Tarentula exasperans</i>	1I, 1F	; AE
<i>T. exasperans</i> (prob.)	1U	; A'
<i>Dictyna borealis</i>	1M	; ?AD
<i>Xysticus deichmanni</i>	3IM, 1IF, 1IU	; 1IMA', rest AE
Noctuidae	16I	; OG
<i>Boloria polaris</i>	2U	; NG
Lycaenidae	5I	; OG
Chironomidae	many mainly F	; most N, G
<i>Limnophyes</i> sp. or spp.	2M, 19F	; 2 ME, 3FD, 16FE
<i>Metrocnemius ursinus</i>	few	; QG (1966)
<i>Paraphaenocladus despectus</i>	5M, 15F	; 5M?C?NE, 8FN?CD, 7FN?CE
<i>Smittia</i> sp. or spp.	4M	; ?CE
<i>S. velutina</i>	479F	; 138ND, 119NE, some? C
<i>Bradysia</i> sp. or spp.	2F	; ND
Syrphidae	9U	; 4PG, 2NG, 3QG
<i>Carposcalis carinata</i>	10M, 6F, 3U	; 2MND, 2MA'G, 6MPD, 6FPD, 3UQG



*Saxifraga oppositifolia* (contd.)

<i>Phalacrodira nigropilosa</i>	8M, 10F, 1U	; 3MA'G, 3MND, 3MN & PG, 1MBD, 1MQE, 1FA'G, 2FPD, 1UA'G
<i>Metasyrphus chillcotti</i>	1M, 1F, 1U	; MPD, FBE, UPG (R1)
Calliphoridae	many	; NG
<i>Boreellus atriceps</i>	18M, 19F, many U	; 4MQG, 7MND, 6MNE, 1MNG, 3FQG, 13FNE, 2FNG, 3FQG, many UNG
<i>Phormia terraenovae</i>	2M	; NG
<i>Periscepsia</i> sp.	1M	; ND (R2)
<i>Scatophaga</i> sp. or spp.	3U	; N
<i>S. apicaulis</i>	10 M, 5F, 6U	; 5MNG, 2MBD, 1MA'G, 2MFCG, 1FNE, 1FNG, 1FQG, 4UNG, 2UA'G
<i>Fucellia pictipennis</i>	2M, 1F, 4U	; 2MNE, FQD, 4UQG
<i>Eupogonomyia groenlandica</i>	1F	; NG
<i>Nematus</i> sp.	1U	; ND
<i>Bombus</i> sp. or spp.	see text	

References: 7, 8, 10, 11, 13, 15, 21, 22, 23, 25, 28, 29

(R1) unanthesed flower, trying P

(R2) also visited pistillate catkin of *Salix arctica*

*Saxifraga rivularis*

Reference: 8

*Saxifraga tricuspidata*

<i>Tipula arctica</i>	1U	; ?NG (1966)
Muscidae	1U	; QG
<i>Bombus</i> sp.	1Q	; N (1966)

*Potentilla nivea*

<i>Bryobia "praetiosa"</i>	several	; QG (R1)
<i>Dictyna borealis</i>	1IM	; AE
Moths	2U	; NG (R2)
Noctuidae	1U	; N
<i>Anarta richarsoni</i>	1U	; NG
<i>Plebius aquilo</i>	1U	; NG
Chironomidae	2U	; QG
Orthocladinae ? gn.	1M	; QD
<i>Smittia</i> spp.	2F	; ?BE





*Potentilla nivea* (contd.)

<i>S. velutina</i>	1F	; ND
<i>Microspectra</i> sp.	1F	; QD
<i>Bradysia</i> 2 spp.	2F	; ND
<i>Rhamphomyia filicauda</i>	2F, 1U	; 1FND, 1FQE, 1UQG
<i>R. nigrita</i>	1F	; ND
<i>Carposcalis carinata</i>	1M	; ?P?D
<i>Phytomyza</i> sp. prob. <i>erigerontophaga</i>	1U	; ND
Tachinidae	2U	; NG
<i>Peleteria aenea</i>	1M	; ?NG
<i>Pogonomyoides segnis</i>	2F	; 1ND, 1?PE
<i>Eupogonomyia groenlandica</i>	1M, 1F	; FND, MQE
<i>Bombus polaris</i>	see text	

References: 10, 11, 23, 30, 34, 35

(R1) also on other parts of plant

(R2) may be *Olethreutes* sp.

(R3) see *Prosmittia nanseni*

*Potentilla* spp.

References: 11, 18, 23

*Dryas integrifolia*

<i>Bryobia "praetiosa"</i>	2U	; QG
<i>Erigone psychrophila</i>	1F	; ?AD
<i>Xysticus deichmanni</i>	2IM, 5F, 3IF, 3U	; 2IMAD, 3FAD, 2FA'D, 2IFAE, 1IFAD
<i>Apatania zonella</i>	1F	; QG
Lepidoptera	1I	; ?OG
Moth	1U	; NG
<i>Byrdia</i> sp.	1I	; OG
Noctuidae	10U	; 5NG, 5QG
<i>Anarta richardsoni</i>	4M, 6U	; 3MND, 1MNG, 5UNG, 1UQG
<i>Crymodes exulis</i>	2M	; 1ND, 1NG
<i>La siestra leucocycla</i>	2M, 2F, 1U	; 2MND, 1FNE, 1FND, 1UNG
<i>Sympistris labradoris</i>	9I	; OG
<i>Boloria chariclea</i>	1M, 8U	; 1MN & BD, 6UN & BG, 1UNG
<i>B. polaris</i>	2M, 1F, 3U	; 2MND, 1FND, 2UN & BG, 1UNG
<i>Boloria</i> sp.	1I	; OG
<i>Colias hecla</i>	1U	; N & BG



*Dryas integrifolia* (contd.)

Nematocera	1M, 10F	; QG
Chironomidae	1F, 1U	; QD
<i>Procladius</i> sp.	1F	; QG
<i>Corynoneura scutellata</i>	2F	; ?ND
<i>Cricotopus</i> sp.	1F	; QE
<i>Limmophyes</i> sp. or spp.	3F	; 2FQD, 1FQG
Orthocladiinae ? gn.	1M, 3F	; MA'E, 2FQD, 1FQE (R2)
<i>Psectrocladius</i>	1F	; QG
<i>Smittia</i> sp. or spp.	3M, 8F	; 2MQD, 1MQE, 5FQD, 1FND, 2FQE
<i>S. velutina</i>	5F	; 1FNE, 3FQE, 1FQD
<i>Microspectra groenlandica</i>	1M	; QE
<i>Forcipomyia</i> ( <i>Thryridomyia</i> ) sp.	1F	; N
<i>Ceratopogon</i> ( <i>Ceratopogon</i> ) sp.	1F	; QG
<i>C. (Isohelea)</i> sp.	1M, 1F	; QG
<i>Culicoides</i> sp.	2M, 1F	; 1MQE, 1MQG, 1FQG
<i>Aedes</i> sp. or spp.	14M, 7F	; 6MNG, 2MBG, 1MN & BD, 5MQG, 3FNG, 4FQG
<i>A. impiger</i>	1M, 1F	; 1MQD, 1FQD
<i>A. nigripes</i>	10M, 8F	; 4MND, 2MNE, 1MN & BD, 3MQD, 2FND, 2FNE, 2FBD, 1FBE, 1FA'D, 1FQD
<i>Bradysia</i> sp. or spp.	2M, 9F, 2U	; 1MQD, 1MQE, 1FNG, 4FQE, 2FQD, 2FQG, 2UQG
Empididae	2OU	; 1NG, 4BG, 15QG
<i>Rhamphomyia filicauda</i>	57M, 145F, 20U	; 4MND, 2MA'D, 18MBD, 31MQD, 2MBE, 8FND, 17FBD, 4FBE, 90FQD, 16FQE, 16UBG, 4UQG
<i>R. hoeli</i>	6M, 29F, 1U	; 6MQD, 2FND, 1FBD, 18FQD, 8FQE, 1UBG
<i>R. nigrita</i>	9M, 24F, 20U	; 4MN & BD, 1MN & BE, 1MBE, 4MQD, 2MQE, 6FND, 1FBD, 13FQD, 4FQE, 7UNG, 3UBD, 7UBG, 2UQG
<i>R. ursinella</i>	1F	; QD
<i>Carposcalis carinata</i>	7M, 18F	; 3MB & PD, 3MPD, 1MQD, 1FN & PD, 4FP & BD, 1FBD, 9FPD, 2FQD, 1FPE
<i>Metasyrphus chillcotti</i>	1M	; PD
<i>Helophilus borealis</i>	1M, 1U	; 1MND, 1UNG (R2)
<i>Allopiophila fulviceps</i>	1F	; QG
<i>Lasiopiophila pilosa</i>	1U	; QG



*Dryas integrifolia* (contd.)

Tachinidae	2U	; NG
<i>Periscepsia</i> sp.	1F	; NG
<i>Peleteria aenea</i>	2M, 1F	; 1MND, 1MNE, 1FQD
Muscidae (excl. <i>Scatophaga</i> spp.)	1F, 16U	; 1FNG, 9UBG, 3UNG, 4UQG
<i>Scatophaga apicaulis</i>	1F	; ?BD
<i>Pegomyia</i> sp.	1F	; QD
<i>P. arctica</i>	1F	; QD
<i>Eopogonomyia groenlandica</i>	3M, 19F	; 1MQD, 2MA'G, 2FPD, 1FQE, 1FQD
<i>Pogonomyoides segnis</i>	7M, 19F	; 1MND, 4MQD, 1MQE, 1MBD, 10FPD, 5FQD, 2FN & PD, 1FQE, 1FQD
<i>Spilogona</i> sp. or spp.	3M, 1F	; 1MQD, 1MA'D, 1MA'G, 1FND
<i>S. denudata</i> (R3)	2M, 1F	; 1MND, 1MQD, 1FQD
<i>S. dorsata</i> (R3)	1F	; QD
<i>S. extensa</i> (R3)	1F	; QE
<i>S. latilamina</i> (R3)	3F	; QD
<i>S. melanosoma</i> (R3)	3M, 10F	; 2MQD, 1MNE, 3FND, 6FQD, 1FA'G
<i>S. obsoleta</i> (R3)	1F	; QD
<i>S. sanctipauli</i> (R3)	26M, 11F	; 5MND, 19MQD, 1MQE, 1MBD, 2FND, 1FBD, 8FQD
<i>S. tornensis</i> (R3)	1F	; QD
<i>S. tundrae</i> (R3)	2M, 3F	; 1MND, 1MBD, 1FBD, 1FQD, 1FQE
Ichneumonidae	1U	; QG
<i>Apanteles</i> sp.	1F	; 1QG
<i>Mesoleius</i> sp.	2M	; 1QE, 1A'E
<i>Saotis</i> sp.	2F	; 1NG, 1QD
<i>Stenomacnis</i> sp.	1M, 1U	; MQD, UQG
<i>Bombus</i> spp.	see text	

References: 2, 4, 10, 11, 15, 23, 25, 26, 28, 29, 36

(R1) one female is "*Prosmittia nanseni*", see text

(R2) visited several flowers

(R3) see text for qualification of names

*Epilobium latifolium*

*Boloria* sp. 1U ; BG (1968)

*Bombus* sp. or spp. see text

References: 11, 19, 21, 25, 28

*Cassiope tetragona*

Chironomidae 1U ; QG (1968)

*Bombus* sp. see text



*Cassiope tetragona* (contd.)

References: 8, 10, 11, 15, 28, 34, 37

*Pedicularis capitata*

<i>Limmophyes</i> sp.	1U	; QG	(1966)
<i>Bombus</i> sp. or spp.	see text		

References: 11, 25, 28

*Pedicularis arctica*

<i>Boloria chariclea</i>	a few	; N	(1966, 1968)
<i>Corynoneura scutellata</i>	4F	; 1?ND, 1?NE, 2?NG	
<i>Limmophyes</i> sp. or spp.	4M, 28F	; 28F?NE, 4MQ?CE	
<i>Paraphaenocladus</i>			
<i>despectus</i>	1F	; NE	
<i>Smittia</i> sp.	1F	; ?NG	
<i>S. velutina</i>	3F	; NE	
<i>Trisocladius</i> sp.	1F	; QG	
<i>Ceratopogon (Isohelea)</i>	1F	; ?NG	
<i>Aedes</i> sp.	1F	; tried N (R1) G	
<i>Bradysia</i> sp. or spp.	1M, 5F	; MNE, FNE	
<i>Rhamphomyia hoeli</i>	1M, 2F	; MNE, 1FND, 1FNE	
<i>Bombus</i> spp. (R2)	see text		

References: 11, 15, 25, 28, 29, 30

(R1) tried 3 times, proboscis too short

(R2) mainly *B. polaris* workers

*Pedicularis hirsuta*

<i>Limmophyes</i> sp. or spp.	(1966)
<i>Smittia velutina</i>	(1966)
<i>Bombus</i> sp. or spp.	see text

References: 1, 5, 6, 7, 8, 11, 27, 30

*Pedicularis sudetica*

Reference: 7





*Erigeron compositus*

Chironomidae	1U	; QG
<i>Rhamphomyia</i> sp.	1U	; QG (1968)
<i>Phytomyza erigerontophaga</i>	3M, 1F, 1U	; ?B?C (waiting, R1) G

References: 11, 23

(R1) copulating pair collected in 1968

*Erigeron eriocephalus*

<i>Limmophyes</i> sp.	1M	; QG
-----------------------	----	------

*Chrysanthemum integrifolium*

Empididae	1U	; NG (1968) (R1)
Syrphidae 2 spp.		(1968) (R1)

(R1) at Tanquary Fiord

*Arnica alpina*

<i>Dictyna borealis</i>	1IM	; AE
<i>Xysticus deichmanni</i>	1IM, 1IF, 26U	; 1IMAD, 1IFAD, 1UA'G, 25UAG
Moth	1U	; NG
Noctuidae	17U	; 2NG, 11QG, 4?BG
<i>Anarta richardsoni</i>	1M	; (R1) E
<i>Crymodes exulis</i>	7M, 1F	; 1MND, 5M?B, 1M?BE, 1FQD
<i>Lasiestra leucocycla</i>	4M, 5F	; 1MND, 1MNE, 1MQD, 1MQE, 1FND, 4FQD
<i>Colias hecla</i>	2M, 8U	; 1MND, 1MQE, 3UNB, 3UN(R2)G, 2UBG
<i>Boloria chariclea</i>	3M, 2F, 25U	; 2MNBD, 1MBD, 2FBD, 14UNBG, 10UBG, 1UQG
<i>Lycaena feildeni</i>	1U	; NBG
<i>Plebius aquilo</i>	1F, 3U	; 1FNBE, 2UBG, 1UNG
<i>Cricotopus</i> sp.	2F	; QG
<i>Heterotrissocladius</i> <i>subpilosus</i>	5F	; 4QD, 1QE
<i>Protanypus caudatus</i>	2M	; 1QD, 1QG
<i>Culicoides</i> sp.	1F	; QG
<i>Aedes</i> sp.	1M	; QG
<i>A. nigripes</i>	2M	; QD
<i>Bradysia</i> 2 spp.	2F	; 1NE, 1QE



*Arnica alpina* (contd.)

<i>Rhamphomyia</i> sp.	1U	; A'QG
<i>R. filicauda</i>	2M, 3F, 1U	; 1MND, 1MQD, 3FQD, 1UQG
<i>R. nigrita</i>	4M, 1U	; 3MND, 1MQD, 1UND
<i>Helophilus borealis</i>	1F	; ND
Calliphoridae	28U	; NG
<i>Boreellus atriceps</i>	2F	; ND
Tachinidae	17U	; 14QG, 3NG (R2)
<i>Peleteria aenea</i>	4M, 3F	; 2MND, 1MNG, 1MQG, 1FND, 2FBD
Muscidae	11U	; 2NG, 9QG
<i>Eupogonomyia groenlandica</i>	1M	; A'E
<i>Pogonomyoides segnis</i>	1F	; ?PD
Ichneumonidae	1U	; QG (R4)
<i>Mesoleptus</i> sp.	1M	; NG
<i>Bombus</i> sp. or spp.	see text	

References: 11, 26, 28

(R1) missed inflorescence, blown by wind

(R2) visited 3 inflorescences

(R3) visited several inflorescences

(R4) scared off before engaging in activity

*Taraxacum arctogenum*

Moths (R1)	3U	; NG
<i>Olethreutes inquietana</i>	1M	; QG
<i>Anarta richardsoni</i>	1F	; ND
<i>Colias hecla</i>	1M	; NE
<i>Boloria chariclea</i>	1U	; NG
<i>Lycaena feildeni</i>	1?F, 1U	; 1?FNE, 1UQG
<i>Boreellus atriceps</i>	1F	; ND
Tachinidae	1U	; QG
<i>Scatophaga</i> sp.	2U	; NG
<i>Bombus</i> spp.	see text	

(R1) probably *Olethreutes* sp.

*Taraxacum* spp.

References: 7, 11, 26



APPENDIX III

TEMPERATURES IN FLOWERS



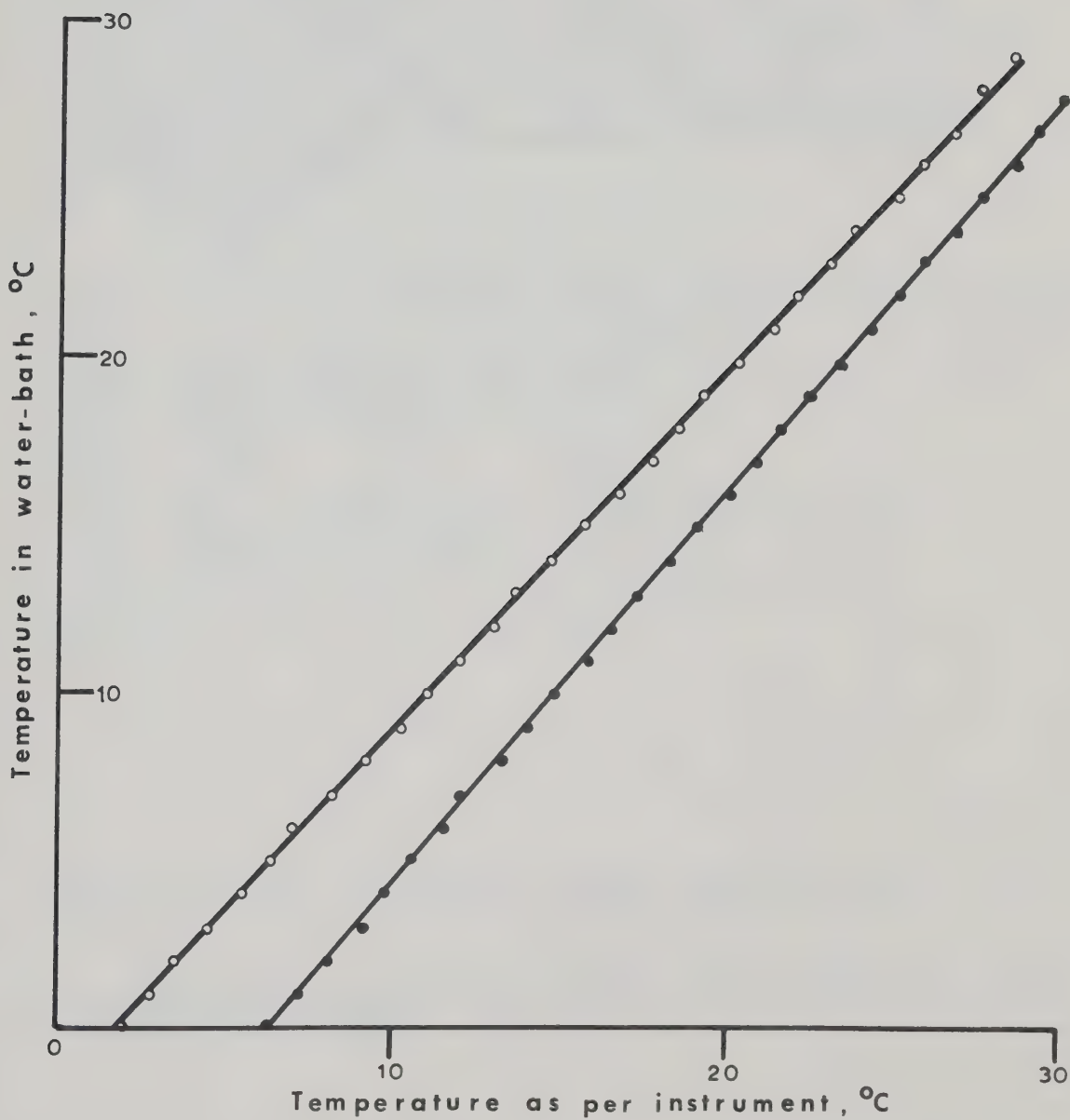




Appendix III-1.

Calibration of temperature measuring instruments against pre-calibrated mercury bulb thermometer in a water bath. Ice water served as reference for thermocouple readings.

open circles; thermocouples  
closed circles; thermistors





## Appendix III-2 Statistical Methods.

The Student's t test was used to test for significance between the means of temperatures within flowers and insects in different positions and under different conditions. The test used was designed for data with unequal variances and sample sizes. Mr. J. Redfield, Zoology Department, University of Alberta, kindly provided me with the computer program (below) and modified it to my needs. I used the IBM APL/360 computer, through the courtesy of the Department of Computing Science, University of Alberta.

The program:

```

      TT[1]
      V TT P;MV;MP;S1;N1;N2;S2;TC;T1;T2;T
[1] ~ T←(MV-MP)÷(((S1÷(+(V-MV÷((+/V)÷N1)))*2)÷N1-1)÷N1+ρV)
      +((S2÷(+(P-MP÷((+/P)÷N2)))*2)÷N2-1)÷N2+ρP)*0.5
[2] TC←(T1+TAB[N1-1]),T2+TAB[N2-1]
[3] TC←(((S1÷N1)×T1)+((S2÷N2)×T2))÷((S1÷N1)+(S2÷N2))
[4] 'S S      ';N1;'      ';N2
[5] 'MEANS      ';MV;'      ';MP
[6] 'VARS      ';S1;'      ';S2
[7] 'S D      ';S1*0.5;'      ';S2*0.5
[8] 'S E      ';(S1÷N1)*0.5;'      ';(S2÷N2)*0.5
[9] 'CALC T=      ';|T
[10] 'SIGNIF LEVEL T =      ';|TC
[11] ~

```

TAB is the table of t values at the 95% confidence level.

Significance in differences between means was taken on  $P < .05$  unless otherwise stated.



Key to Symbols in Appendices III-3 to III-8.

under conditions:

C = cloudy  
c = high alto-cirrus  
E = mounted on board  
F = field observations  
I = whole flower  
L = sun low (time of day)  
O = optimal weather  
P = decorollate flower  
S = desporophyllate flower  
T = t test done with experiment in question  
t = t test done to compare with other experiments  
W = windy (> 2 mps)  
w = light breeze (1-2 mps)

in test tables

S = significantly different,  $P < .05$   
S\* = significantly different,  $P < .10$   
I = not significantly different,  $P > .10$

after appendix number

e = temperature in inflorescences in terms of temperature  
excess (above ambient)  
a = temperature of inflorescence measured directly

All temperatures in degrees Centigrade





Appendix III-3.

Temperatures in microgreenhouse flowers. Key

<u>Appendix number</u>	<u>Species of flower</u>	<u>Date</u>	<u>Conditions</u>
III-3-1	<i>Pedicularis arctica</i>	28.VII.1966	O E T
-2		28.VI. 1967	O E T
-3		15.VII.1967	C E T
-4		9.VII.1966	C F
-5		17.VII.1968	O F
-6		28.VII.1968	C E T
III-3-7	<i>P. capitata</i>	26.VII.1966	O E T
-8		16.VII.1966	C E T
-9		7.VII.1968	O F
III-3-10	<i>Melandrium apetalum</i>	17.VII.1968	O F
-11		28.VII.1966	O E
-12		19.VII.1968	C F T
III-3-13	<i>M. triflorum</i>	7.VII.1968	O F
-14		5.VII.1968	W O F
-15		17.VII.1967	O E
-16		28.VII.1968	C F



[illegible]



		Angle of incidence of solar radiation							Ambient
	0	45	90	135	180	225	270	315	
	S		W		N		E		
Appendix III-3-8 e									
Mean	0.1		0.05		0.1		0.1		
Max.	0.25		0.25		0.25		0.25		
Min.	0		0		0		0		
S.D.	0.13		0.11		0.04		0.04		
N	9		9		9		9		
Appendix III-3-9 e									
Mean	3.9								14.0
N	15								

		0	45	90	135	180	225	270	315		
t test III-3-1	0		I	S	S	S	S	S	I	t test III-3-2	
	45	I		S	S	S	S	I	I		
	90	I	I		S	S	S	I	I		
	135	I	I	I		I	I	S	S		
	180	S	S	S	S		I	S	S		
	225	I	I	I	I	I		S	S		
	270	I	I	I	I	S	I		S		
	315	I	I	I	I	S	I	I			





		0	45	90	135	180	225	270	315		
		0	I	S	S	S	I	I	S		
t test	45	I		I	S	S	S	I	I	t test	III-3-7
III-3-3	90	I	I		S	S	S	I	I		
III-3-6	135	I	I	I		I	I	S	S		
III-3-8	180	I	I	I	I		I	S	S		
		225	I	I	I	I		S	S		
		270	I	I	I	I	I		I		
		315	I	I	I	I	I	I			



			Corolla	Ambient	
Appendix	III-3-10	a			
	Mean		20.9	15.7	
	Max.		23.3	17.0	
	Min.		19.0	15.0	
	S.D.				
	N		11	11	
Appendix	III-3-11	e			
	Mean		2.5		
	Max.		2.5		
	Min.		2.5		
	N		3		
Appendix	III-3-12	a			
	Mean		15.04	14.97	not significantly different
	Max.		16.0	15.75	
	Min.		14.5	13.5	
	S.D.		0.43	0.52	
	N		11	24	
Appendix	III-3-13	e			
	Mean		6.2	14.8	
	Max.		9.5		
	Min.		4.7		
	N		10		
Appendix	III-3-14	a			
	Mean		12.8	10.7	
	Max.		14.5	12.0	
	Min.		10.25	9.25	
	S.D.		1.28	1.23	
	N		18	10	
Appendix	III-3-15	e			
	Mean		4.25	17.5	
	Max.		4.75		
	Min.		2.75		
	S.D.		0.66		
	N		9		
Appendix	III-3-16	a			
	Mean		6.7	6.25	
	Max.		7.0	6.75	
	Min.		6.25	5.75	
	S.D.		0.31	0.71	
	N		4	2	



III-4.

Intrafloral temperatures in hairy heat traps, *Salix arctica*  
in florescences (f = pistillate, m = staminate)

<u>Appendix number</u>	<u>Sex of catkin</u>	<u>Date</u>	<u>Conditions</u>
III-4-1	f	29.VI.1967	O E T t
-2	f	29.VI.1968	O F T t
-3	f	29.VI.1967	O F T
-4	f	21.VI.1968	O F T
-5	f	22.VI.1968	W O F T
-6	f	24.VI.1968	C F T
-7	f	29.VI.1966	O E
III-4-8	m	24.VI.1968	C F T
-9	m	29.VI.1967	O E T t
-10	m	29.VI.1966	O E
-11	m	29.VI.1968	O F T t
-12	m	22.VI.1968	W O F T
-13	m	21.VI.1968	O F T
-14	m	27.VI.1967	w O E T
III-4-15	m and f	26.VI.1966	W C F



Angle of incidence of solar radiation					
	S	W	N	E	Ambient air
Appendix III-4-1	e				
Mean	2.75	1.79	0.75	2.04	11.5
Max.	4.75	3.75	1.75	4.0	
Min.	1.25	0	0	1.0	
S.D.	1.33	1.26	0.84	1.09	
N	6	6	6	6	
Appendix III-4-2	e				
Mean	6.2		1.7		9.0 S & N significantly different
Max.	8.25		2.0		
Min.	3.25		1.5		
S.D.	1.58		0.24		
N	8		4		
Appendix III-4-3	e				
Mean	5.5		0.6		11.5 S & N significantly different
Max.	8.5		3.75		
Min.	2.5		0		
S.D.	2.08		1.22		
N	11		11		
Appendix III-4-4	a				
Mean	13.97		12.91		11.0 S & N significantly different
Max.	17.75		16.0		12.75
Min.	8.5		8.5		6.9
S.D.	2.85		2.31		2.46
N	8		8		6
Appendix 4-5	a				
Mean	11.9		10.1		7.4 S & N significantly different
Max.	14.25		11.75		7.5
Min.	9.5		9.25		7.25 S & N both significantly different
S.D.	1.32		0.86		0.14
N	10		10		4 from ambient
Appendix 4-6	a				
Mean	6.1		6.2		6.1 S & N & ambient
Max.	7.5		7.5		7.25 are all not significantly different
Min.	5.0		5.0		4.75
S.D.	0.34		0.36		0.39
N	10		10		10
Appendix III-4-7	e				shaded catkin
Mean	5.0		6.6		9 1.7
Max.	7.0		7.5		2.0
Min.	3.25		6.0		1.5
N	3		4		4





	S	W	N	E	Ambient	
Appendix III-4-8	a					
Mean	6.7		6.9		6.5	S & N & ambient
Max.	7.0		7.25		6.75	are not signifi-
Min.	6.25		6.5		6.25	cantly different
S.D.	0.27		0.28		0.25	
N	5		5		5	
Appendix III-4-9						
Mean	5.6		1.9		11.5	S & N are signi-
Max.	7.0		2.0			fificantly different
Min.	4.0		1.5			
S.D.	1.26		0.25			
N	4		4			
Appendix III-4-10	e				shaded	
Mean	4.3		4.2		9	1.2
Max.	6.3		6.0			2.0
Min.	3.0		2.5			1.3
N	3		3			3
Appendix III-4-11	e					
Mean	4.2		1.7		9	S & N are signi-
Max.	6.3		2.0			fificantly different
Min.	2.5		1.3			
S.D.	1.57		0.38			
N	6		3			
Appendix III-4-12	a					
Mean	12.9		12.3		9.9	S & N are not sig-
Max.	14.25		13.75		10.25	nificantly different
Min.	11.75		11.0		9.5	but both are signi-
S.D.	0.97		1.01		0.37	fificantly different
N	10		10		4	from ambient
Appendix-III-4-13	a					
Mean	15.25		14.7		12.5	S & N are not sig-
Max.	23.0		19		18.0	nificantly different
Min.	10.25		9.75		7.9	& do not differ sig-
S.D.	3.91		3.51		3.24	nificantly from
N	10		10		8	ambient
Appendix-III-4-14	a					
Mean	3.8	3.6	3.6	4.4	13	
Max.	7.5	7.5	7.3	7.8		
Min.	2.0	1.3	1.8	2.8		
S.D.	1.56	1.83	1.52	1.54		
N	14	14	14	14		



Appendix III-4-15 e	m	f
Mean	0	0
Max.	0	0
Min.	0	0
S.D.	0	0
N	6	6



		S	W	N	E	
	S		I	I	I	
t test III-3-1	W	I		I	I	t test III-3-14
	N	S	I		I	
	E	I	I	I		

t tests *Salix* m to f

- III- 4- 9 TT EEE- 4-1 non insolated sides (N) not significantly different; insolated side (S) significantly different
- III-4-11 TT III-4-2 non insolated sides (N) not significantly different; insolated sides (S) significantly different at .90 level





III-5.

Intrafloral temperatures in hanging bells, *Cassiope tetragona*

<u>Appendix number</u>	<u>Date</u>	<u>Conditions</u>
III-5-1	17.VII.1968	O F
-2	22.VI.1967	O F
-3	30.VI.1967	s O F
-4	1-2.VII.1968	L O F



			Ambient	
Appendix III-5-1	e			
Mean	3.7		16.3	
N	14			
Appendix III-5-2	e			
Mean	0.8	8.0	Corolla temperature	
Max.	1.8		differs significantly	
Min.	0		from ambient	
S.D.	0.56			
N	12			
Appendix III-5-3	e			
Mean	0.5	7.0		
Max.	1.0			
Min.	0			
S.D.	0.27			
N.	8			
Appendix III-5-4	a			
Mean	10.6	9.8	Corolla temperature does	
Max.	13.25	11.25	not differ significantly	
Min.	8.25	8.0	from ambient	
S.D.	1.58	1.32		
N	33	6		



Appendix III-6.

Intrafloral temperatures in discs.

<u>Appendix number</u>	<u>Species of inflorescence</u>	<u>Date</u>	<u>Conditions</u>
III-6-1	<i>Taraxacum arctogenum</i>	28.VII.1966	O E T
-2		17.VII.1967	c O E
-3		1-2.VII.1968	L O F T
-4		7.VII.1968	O F
III-6-5	<i>Arnica alpina</i>	17.VII.1967	c O E
III-6-6	<i>Erigeron compositus</i>	7.VII.1968	O F
-7		5.VII.1968	W O F T



Angle of incidence of solar radiation (multiples of shadow length)  
Ambient

	<u>0x</u>	<u>1x</u>	<u>2x</u>	<u>4x</u>	<u>8x</u>	<u>inf.</u>	<u>Shade</u>	<u>air</u>
Appendix III-6-1 e								
Mean	3.1	2.0	1.8	0.5	0.6	0.3	0.3	
Max.	3.3	2.3	2.8	1.0	1.3	0.5	0.5	
Min.	2.8	1.8	1.3	0	0	0	0	
S.D.	0.24	0.20	0.67	0.29	0.60	0.20	0.20	
N	4	4	4	4	4	4	4	
Appendix III-6-2 e								
1 head only	5.0	3.0	1.0	0.5	--	0.0	0.0	17.5
Appendix III-6-3 a								
Mean	11.5		Temperature in inflorescences					9.5
Max.	17.3		differs significantly from					11.0
Min.	8.8		ambient					8.3
S.D.	2.37							1.22
N	18							5
Appendix III-6-4 a								
Mean	23.5							20.5
Max.	27.0							
N	10							
Appendix III-6-5 e								
1 head only	4.9	3.3	1.5	0.8	--	0.0	0.0	17.5
N	4	1	1	1	--	1	3	
Appendix III-6-6 e								
Mean	6.2							18.0
Max.	11.0							
Min.	4.5							
N	20							
Appendix III-6-7 a								
Mean	14.6		Temperature in inflorescence					11.6
Max.	17.3		is significantly higher than					12.0
Min.	11.0		ambient					10.8
S.D.	1.50							0.72
N	30							3





	0	1	2	4	8	inf.	shade
t test							
III-6-1							
0							
1	S						
2	S	I					
4	S	S	S*				
8	S	S	S*	I			
inf.	S	S	S	I	I		
shade	S	S	S	I	I	I	

\* S at 90% level



Appendix III-7.

Intrafloral temperatures in paraboloid or bowl-shaped flowers.

<u>Appendix number</u>	<u>Species of flower</u>	<u>Date</u>	<u>Conditions</u>
III-7-1	<i>Dryas integrifolia</i>	14.VII.1967	O E I
-2		8.VII.1967	w O E I T t t
-3		26.VII.1966	O E I T t
-4		28.VI. 1967	O E I
-5		27.VI. 1967	O E I T
-6		26.VII.1966	O E P T t
-7		8.VII.1967	w O E P T t t
-8		14.VII.1967	O E P
-9		14.VII.1967	O E S
-10		8.VII.1967	w O E S T t t
-11		5.VII.1967	w O F I t
-12		5.VII.1967	w O F S t
-13		7.VII.1968	O F I
-14		7.VII.1968	O F I
-15		5.VII.1968	w O F I T
-16		16.VII.1967	C E I
-17		14.VII.1967	c O F I
III-7-18	<i>Potentilla nivea</i>	17.VII.1967	O E I
-19		28.VII.1966	O E I
-20		comb. of 18 & 19	O E I
-21		5.VII.1968	O F I
III-7-22	<i>Papaver radicatum</i>	28.VII.1967	O E I
-23		7.VII.1968	O F I
-24		16.VII.1966	C F I
-25		28.VI. 1968	C F I T



Angle of incidence of solar radiation (multiples of shadow length)

	<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>inf.</u>	<u>Sh.</u>	Ambient air
Appendix III-7-1	e							
Mean	5.1	4.9	4.4	3.4	1.6	0.9	0.0	9.0
Max.	5.3	5.0	4.5	3.8	1.8	1.0	0.0	
Min.	5.0	4.8	4.3	3.0	1.5	0.8	0.0	
N	2	2	2	2	2	2	4	
Appendix III-7-2	e							
Mean	3.9	3.0	2.6	1.5	1.0	0.7	0.0	4.0
Max.	4.3	3.3	2.8	1.8	1.0	0.8	0.0	
Min.	3.3	2.8	2.3	1.3	0.8	0.5	0.0	
S.D.	0.45	0.18	0.21	0.21	0.11	.06	0.0	
N	5	5	5	5	5	5	5	
Appendix III-7-3	e							
Mean	6.5	5.8	4.7	1.7	1.3	1.0	0.4	12.5
Max.	7.8	7.8	5.5	2.3	1.8	1.5	0.8	
Min.	4.3	3.5	2.8	0.8	0.8	0.5	0.3	
S.D.	0.93	1.33	0.92	0.49	0.32	0.33	0.18	
N	20	10	10	10	10	10	10	
Appendix III-7-4	e							
Mean	4.75	4.0	2.5	1.5	1.0	1.0	0	10.5
N	1	1	1	1	1	1	1	
Appendix III-7-5	e							
Mean	6.8	5.6	4.7	3.4	2.1	1.0	0.2	13
Max.	8.3	6.8	6.3	4.3	3.3	1.3	0.5	
Min.	6.0	4.5	2.5	1.5	0.8	0.8	0.0	
S.D.	1.06	0.92	1.57	1.27	1.20	--	--	
N	4	4	4	4	4	4	4	
Appendix III-7-6	e							
Mean	4.0	3.7	2.5	1.5	0.7	0.4	0.3	12.5
Max.	5.3	5.3	3.0	1.8	0.8	0.5	0.3	
Min.	2.5	2.3	1.8	1.3	0.5	0.3	0.3	
S.D.	1.10	1.15	0.47	0.21	0.14	0.14	0.0	
N	10	5	5	5	5	5	5	
Appendix III-7-7	e							
Mean	1.5	1.6	1.3	1.1	0.9	0.7	0.0	4.0
Max.	1.8	1.8	2.0	1.5	1.3	0.8	0.0	
Min.	1.3	1.3	0.8	0.8	0.5	0.5	0.0	
S.D.	0.17	0.19	0.39	0.28	0.28	0.12	0.0	
N	7	7	7	7	7	7	7	
Appendix III-7-8	e							
Mean	3.3	3.1	3.3	1.8	1.6	1.9	0.0	9.0
Max.	3.3	3.3	3.3	1.8	1.8	2.0	0.0	
Min.	3.3	3.0	3.3	1.8	1.5	1.8	0.0	
N	2	2	2	2	2	2	2	





	<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>inf.</u>	<u>Sh.</u>	<u>Ambient air</u>
Appendix III-7-9 e								
Mean	4.6	4.6	4.0	2.9	1.6	0.9	0.0	9.0
Max.	4.8	4.8	4.0	3.0	1.8	1.0	0.0	
Min.	4.5	4.5	4.0	2.8	1.5	0.8	0.0	
N	2	2	2	2	2	2	2	

Appendix III-7-10 e								
Mean	4.0	2.2	1.6	0.9	0.5	0.1	0.0	4.0
Max.	4.3	2.3	2.0	1.0	0.5	0.3	0.0	
Min.	3.8	2.0	1.5	0.8	0.5	0.0	0.0	
S.D.	0.21	0.11	0.22	0.14	0.0	0.06	0.0	
N	5	5	5	5	5	5	5	

		<u>Ambient air</u>	
Appendix III-7-11 a			
Mean	18.1	12.5	III-7-11 is significantly different from III-7-12
Max.	19.5		
Min.	15.0		
S.D.	1.35		
N	12		

Appendix III-7-12 a		
Mean	16.9	12.5
Max.	18.0	
Min.	15.0	
S.D.	1.0	
N	8	

Appendix III-7-13 a		
Mean	22.3	15.0
Max.	25.5	15.5
Min.	17.5	14.5
N	52	



Direction of incident solar radiation

	<u>S</u>	<u>W</u>	<u>N</u>	<u>E</u>	<u>Ambient air</u>
Appendix III-7-14 a					
Mean	22.4	21.6	19.6	23.1	15
Max.	25.0	24.5	21.3	25.5	15.5
Min.	18.3	18.8	17.5	21.0	14.5
N	20	14	8	10	

Appendix III-7-15 a					
Mean	12.0	11.6	10.7	11.1	8.8
Max.	13.5	12.3	12.3	12.0	9.3
Min.	10.5	10.0	9.8	10.0	8.5
S.D.	0.92	0.67	0.63	0.49	0.35
N	20	20	20	20	4

					<u>Ambient air</u>
Appendix III-7-16 e					
Mean	0.2				
Max.	0.3				
Min.	0.0				
S.D.	0.10				
N	30				

Appendix III-7-17 e					
Mean	3.1			9.0	
Max.	3.8				
Min.	2.5				
S.D.	0.45				
N	12				

	S	W	N	E
	S	I	S	S
t test	W		S	S
III-7-15	N			S



		<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>inf.</u>	<u>sh.</u>	
t test III-7-3	0	S	I	S	S	S	S	S	
	1	I	S	S	S	S	S	S	t test III-7-6
	2	S	S	S	S	S	S	S	
	4	S	S	S	I	S	S	S	
	8	S	S	S	S	S	S	S	
	inf.	S	S	S	S	I	S	I	
	sh.	S	S	S	S	S	S	I	
									III-7-6 vs III-7-3

		<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>inf.</u>	<u>sh.</u>
III-7-5	0							
	1	I						
	2	I	I					
	4	S	S*	S				
	8	S	S	S	I			
	inf.	S	S	S	S	S		
	sh.	S	S	S	S	I	I	



t test III-7-7

	0	1	2	4	8	inf.	Sh.
S		I	I	S	S	S	S
S		S	I	I	S	S	S
S		S	S	I	I	S	S
		S		S*	I	S	S
			I		I	S*	S
				I		I	S
					S		I
						S	I
							I

III-7-2 vs III-7-7

III-7-7 vs III-7-10

t test III-7-10

	0	1	2	4	8	inf.	Sh.
0	I	S	S	S	S	S	S
1	S	S	S	S	S	S	S
2	S	S	S	S	S	S	S
4	S	S	S	S	S	S	S
8	S	S	S	S	S	S	S
inf.	S	S	S	S	S	S	I
Sh.	S	S	S	S	S	S	I

III-7-2 vs III-7-10





	<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>inf.</u>	<u>sh.</u>	<u>Ambient air</u>
Appendix III-7-18 e								
Mean	2.8	1.3	0.7	0	-	-	0	17.5
Max.	3.0	1.5	0.8	0	-	-	0	
Min.	2.5	1.3	0.5	0	-	-	0	
N	3	3	3	3	-	0	3	
Appendix III-7-19 e								
Mean	2.7	1.6	1.6	0.3	0.1	-	0.0	17.5
Max.	3.8	2.0	2.0	0.3	0.3	-	0.0	
Min.	1.5	0.8	0.8	0.3	0.0	-	0.0	
S.D.	0.92	0.59	0.59	0.0	0.12	-	0.0	
N	4	4	4	4	4	0	4	
Appendix III-20 (= 19 + 18) e								
Mean	2.7	1.5	1.2	0.1	0.1	-	0.0	
Max.	3.8	2.0	2.0	0.3	0.3	-	0.0	
Min.	1.5	1.5	0.5	0.0	0.0	-	0.0	
S.D.	0.67	0.44	0.67	0.12	0.13	-	0.0	
N	7	7	7	7	4	0	7	
Appendix III-7-21 a								
Mean	12.4							9.0
Max.	18.0							10.3
Min.	10.0							8.0
S.D.	1.87							0.83
N	30							5
Appendix III-7-22 e								
Mean	5.4	4.8	2.1	0.8	0.5	-	0.5	7.0
Max.	7.0	6.8	3.3	2.0	1.0	-	1.0	
Min.	4.5	2.5	0.8	0.0	0.0	-	0.0	
S.D.	0.85	1.53	0.90	0.80	0.32	-	0.30	
N	7	7	7	7	7	0	7	
Appendix III-7-23								
Mean	23.0							15.8
Max.	26.8							17.5
Min.	19.0							14.0
N	12							4
Appendix III-7-24 e								
Mean	0.3							
Max.	0.5							
Min.	0.3							
S.D.	0.12							
N	10							



Ambient  
air

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Appendix III-7-25 a

Mean	6.0	6.0	No statistical difference
Max.	7.3	7.5	between ambient air &
Min.	4.5	4.5	flower temperatures
S.D.	0.78	0.91	
N	22	11	

	<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>sh.</u>
t test III-7-22	0					
	1	I				
	2	S	S			
	4	S	S	S		
	8	S	S	S	I	
	sh.	S	S	S	I	I



Appendix III-8.

Intraflora temperatures in inverted bells.

<u>Appendix number</u>	<u>Species of flower</u>	<u>Date</u>	<u>Conditions</u>
III-8-1	<i>Saxifraga oppositifolia</i>	21.VI. 1966	O E T
-2		21.VII.1966	O E I T t t
-3		21.VII.1966	O E S T t t
-5		7.VI. 1967	O E T
-6		16.VI. 1966	C F
-7		20- 21.VI. 1968	O F T
III-8-8	<i>Lesquerella arctica</i>	2.VII.1968	L O F
III-8-9	<i>Cerastium alpinum</i>	28.VII.1966	O E T





Angle of incidence of solar radiation (multiples of shadow length)

	<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>Inf.</u>	<u>Sh.</u>	Ambient <u>air</u>
Appendix III-8-1 e								
Mean	2.3	1.8	1.4	1.1	0.7		0.1	10.5
Max.	2.8	2.3	2.0	1.8	1.0		0.5	
Min.	1.3	1.0	0.3	0.8	0.0		0.0	
S.D.	0.50	0.42	0.50	0.38	0.35		0.17	
N	10	10	10	10	10		10	
Appendix III-8-2 e								
Mean	1.4	1.2	0.6	0.1	0.0			12
Max.	1.8	1.3	0.8	0.3	0.0			
Min.	1.3	0.8	0.3	0.0	0.0			
S.D.	0.22	0.22	0.21	0.11	0.0			
N	5	5	5	5	5			
Appendix III-8-3 e								
Mean	0.2	0.1	0.0	0.0	0.0			12
Max.	0.5	0.3	0.0	0.0	0.0			
Min.	0.0	0.0	0.0	0.0	0.0			
S.D.	0.21	0.14	0.0	0.0	0.0			
N	5	5	5	5	5			
Appendix III-8-4 e								
Mean	1.2	0.9	0.3	0.1	0.0			12
Max.	1.5	1.0	0.5	0.3	0.0			
Min.	1.0	0.5	0.3	0.0	0.0			
S.D.	0.22	0.22	0.11	0.11	0.0			
N	5	5	5	5	5			
Appendix III-8-5 e								
Mean	2.7	1.8	0.8	0.5		0.1	0.0	2.0
Max.	4.5	3.0	1.3	0.8		0.3	0.0	
Min.	1.8	1.0	0.0	0.0		0.0	0.0	
S.D.	0.68	0.58	0.29	0.20		0.12	0.0	
N	17	17	17	17		17	17	
Appendix III-8-6 e								
Mean	0.1							
Max.	0.5							
Min.	0.0							
S.D.	0.18							
N	10							
Appendix III-8-7 e								
	<u>S</u>	<u>W</u>	<u>N</u>	<u>E</u>	<u>Z</u>		Ambient <u>air</u>	
Mean	5.8	2.0	0.2	2.6	3.9		13.6	
Max.	14.3	8.8	3.5	11.3	8.0		20.3	
Min.	1.5	-4.3	-5.0	-4.3	1.0		8.3	
S.D.	3.26	2.99	2.21	3.05	2.67		3.25	
N	27	25	29	32	16		16	
Appendix III-8-8 a								
Mean						9.6		
Max.						12.5		
Min.						7.8		
S.D.						1.43		
N						52		



	0	1	2	4	8	sh.	
t test III-8-2	0	I	I	S	S	S	S
	1	I	I	S	S	S	S
	2	S	S	S*	S	S	S
	4		S	I	I	I	I
	8			S	I	I	I
sh.				I	I	I	I

t test  
III-8-4

III-8-2 vs  
III-8-4

III-8-3 vs  
III-8-4

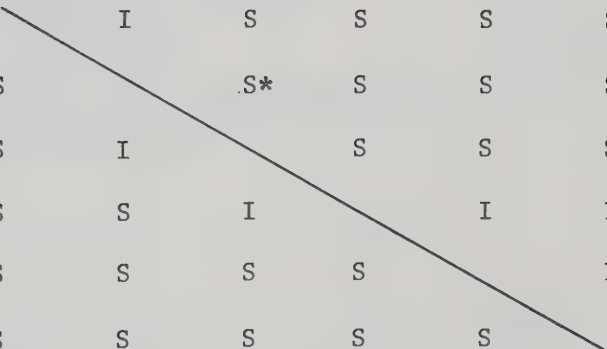
	0	1	2	4	8	sh.	
t test III-8-2	0	S	I	I	I	I	I
	1	I	S	I	I	I	I
	2	S	S	S	I	I	I
	4	S	S	S	I	I	I
	8	S	S	S	I	I	I
sh.	S	S	S	I	I	I	I

t-test  
III-8-3

		Z	S	W	N
t test III-8-7	S	S*			
	W	S*	S		
	N	S	S	S	
	E	I	S	I	S



	<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>Sh.</u>
Appendix III-8-9 e						
Mean	2.1	1.8	1.0	0.1	0.2	0.2
Max.	2.5	2.3	1.3	0.3	0.3	0.3
Min.	1.8	1.3	0.8	0.0	0.0	0.0
S.D.	0.31	0.43	0.29	0.13	0.13	0.13
N	4 4	4	4	4	4	4

		<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>sh.</u>	
t test III-8-1	0						S	t test III-8-9
	1	S	I	S*	S	S	S	
	2	S	I		S	S	S	
	4	S	S	I		I	I	
	8	S	S	S	S		I	
	sh.	S	S	S	S	S		

		<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>inf.</u>	<u>sh.</u>
t test III-8-5	0						
	1	S					
	2	S	S				
	4	S	S	S			
	inf.	S	S	S	S		
	sh.	S	S	S	S	S	



APPENDIX IV

INSECT BODY TEMPERATURES

IV- 1	<i>Aedes nigripes</i>	28.VI. 1967
- 2	<i>Aedes</i> sp.	7.VII.1968
- 3	<i>A. nigripes</i>	19.VII.1967
- 4	<i>Aedes</i> sp.	8.VII.1968
- 5	<i>Rhampomyia filicauda</i>	27.VI. 1967
- 6	<i>R. nigrita</i>	8.VII.1968
- 7	<i>Caroposcalis carinata</i>	8.VII.1968
- 8	<i>Boreellus atriceps</i>	8.VII.1968
- 9	<i>Aedes</i> sp.	7.VII.1968
-10	<i>Aedes</i> sp.	28.VI. 1967
-11	<i>A. nigripes</i>	19.VII.1968
-12	<i>Aedes</i> sp.	8.VII.1968
-13	<i>Rhampomyia filicauda</i>	27.VI. 1967
-14	<i>R. nigrita</i>	8.VII.1968
-15	<i>Caroposcalis carinata</i>	8.VII.1968
-16	<i>Boreellus atriceps</i>	8.VII.1968
-17	<i>Rhampomyia filicauda</i>	27.VI. 1967
-18	<i>R. filicauda</i>	27.VI. 1967

All experiments performed under optimal conditions

Symbols as for Appendix III





	<u>IV-1 e</u>	<u>IV-2 e</u>	<u>IV-3 e</u>	<u>IV-4 e</u>
Mean	5.89	6.08	6.2	10.15
Max.	6.5	8.0	6.5	16.0
Min.	5.3	4.0	5.8	3.5
S.D.	0.47	1.78	-	3.29
N	9	4	2	24

	<u>IV-5 e</u>	<u>IV-6 e</u>	<u>IV-7 e</u>	<u>IV-8 e</u>
Mean	6.14	11.9	13.5	14.4
Max.	9.5	16.5	16.7	17.4
Min.	4.5	8.0	10.3	11.3
S.D.	1.13	2.71	3.70	3.30
N	18	18	4	4

IV-9 e                      N = 2                      (original data lost in transit)

<u>IV-10</u>	in whole flower	in air	
Mean	5.8	4.1	Significantly
Max.	9.5	8.5	different
Min.	6.5	2.7	P < 0.05
S.D.	0.52	0.60	
N	4	4	

IV-11      N = 2      (original data lost in transit)

IV-12      N = 10      (original data lost in transit)      Statistics IV-4 probably apply: then insect body temperature in whole flowers significantly different from in desporophyllate, significantly different from in decorollate, which is significantly different from in air.

<u>IV-13 e</u>	in whole flower	in air	
Mean	5.95	4.75	Do not differ
Max.	6.5	5.0	significantly
Min.	5.3	4.8	P > 0.1
S.D.	2.06	2.22	
N	4	4	

IV-14      N = 10      (original data lost in transit)      Statistics from Appendix IV-6 probably apply: then results as expressed in Appendix IV-12.



IV-15    N = 4    (original data lost in transit)    Statistics from Appendix IV-7 may apply: then results probably as IV-12.

IV-16    N = 4    (original data lost in transit)    Statistics from Appendix IV-8 may apply: then results probably as IV-12.

IV-17   e

Solar angle of incidence (multiples of shadow length)							
	<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>inf.</u>	<u>sh.</u>
Mean	6.16	4.75	3.90	3.25	2.55	1.65	0.05
Max.	9.5	5.8	5.0	4.3	3.0	3.3	0.3
Min.	4.5	3.5	3.0	2.8	2.3	0.8	0.0
S.D.	1.20	1.02	0.80	0.40	0.33	0.38	0.11
N	16	5	5	5	5	5	5

IV-18   e

Mean	6.75	5.62	4.69	3.38	2.13	1.75	0.19
Max.	8.3	6.8	6.3	4.3	3.3	3.3	0.5
Min.	6.0	4.5	2.5	1.5	0.8	0.8	0.0
S.D.	1.06	0.92	1.57	1.27	1.20	1.08	0.24
N	4	4	4	4	4	4	4

		<u>0</u>	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>inf.</u>	<u>sh.</u>		
t test IV-18	0	I	S	S	S	S	S	S	t test IV-17	
	1	I	I	I	S	S	S	S		
	2	I	I	I	I	S	S	S		
	4	S	I	I	I	S	S	S		
	8	S	S	I	I	I	S	S		
	inf.	S	S	S*	I	I	I	S		
	sh.	S	S	S	S	S	S*	I		
									IV-17 vs IV-18	













**B29967**